



B. F. Sergeev

THE WORLD OF THE AMPHIBIANS



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OF

THE AMPHIBIANS

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by M. Rosenberg

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An Ode to the Green Toad

The myriad life forms which make up the world around us are all interdependent. The extinction of even a single organism has an adverse effect on the balance of Nature, though some organisms play a more noticeable and better known part than others. This book discusses the amphibians and the part they play in our ecology.

The amphibians, as we call animals able to live both aquatic and terrestrial lives, have evolved a great variety of forms, and inhabit all the continents of the world today.

Amphibians are active predators, and constitute an important link in the food chain. Extremely voracious, they are natural population regulators of the thousands of invertebrate species that they feed on. In their turn, amphibians are extremely prolific and capable of rapid growth and intensive utilization of available food resources. Thus, they are able to increase their number and biomass very rapidly and so govern the population of the secondary predators who feed on them.

The activity of the amphibians is of remarkable significance in nature. By developing agriculture, sowing vast areas with food and other crops, we create the most favourable conditions for the life and reproduction of all the organisms that feed on plants. And they take advantage of these ideal living conditions and inflict considerable, and sometimes even catastrophic losses on our agriculture. This is when the significance of amphibians may be greatest! Wherever we have not unthinkingly sharply reduced their numbers, they become active defenders of the plants and can help the other enemies of our enemies to save the harvest.

The significance of amphibians for the biosphere of our planet and, consequently, for mankind is so great

that it is difficult to equate it with that of any other group of organisms. Even birds, whose biological role is well-known, are in some ways less important than the amphibians.

The frog (*Rana*) is perhaps the best known of the amphibians, and it, or its close relative the toad (*Bufo*) and the genus *Bombina*, are distributed throughout our planet except for the areas with constantly low air temperatures and extremely dry regions.

Amphibians have inhabited our planet for so long that they have managed to evolve faculties that we, their old friends, are very often unaware of.

The skin of frogs and toads secretes substances containing many different compounds. Some of them, such as poisons, have long been used by man. There are some species of frogs and toads whose poisons are very strong. For example, the poison of many of the tree-frogs of South America is deadly for large animals and humans even in minute doses.

As is well known, poisons in appropriate doses may have a medical application. Ancient Oriental prescriptions mention poisons secreted by the skin of some toads. Scientists today are very interested in frog poisons that reduce the blood pressure of humans, induce vasodilation, stimulate respiration and blood circulation, destroy helminths, accelerate the healing of wounds, and prevent suppuration. The final stage in these investigations should be the synthesis of these extremely complex compounds, which would enable mass production of such drugs.

But why has Nature assisted some species of frogs to acquire a toxic coating? The answer seems to be simple: for defence against enemies! However, recent researches indicate that these dermal poisons are not just for scaring away enemies. Their primary function is defence against microorganisms. Fungi and bacteria settle constantly on

the permanently moist skin of the frog and the dermal secretion protects the animal against these infections.

Some laboratories are working on the extraction of these protective substances. It is not unlikely that in the long run they will replace antibiotics that are losing their effect. A little has been achieved already: an effective drug against skin fungi has been synthesized from the component parts of the frog poison.

Today amphibians are used for research into the genetic apparatus of cells, organ regeneration, tissue compatibility, and many other problems. We shall point out only that the first successful heart transplantation in a frog was performed 35 years ago by Sinitsyn, a Soviet scientist. His experimental frogs with transplanted hearts survived many years and remained perfectly healthy.

A monument to the frog has been erected at the Pasteur Institute in Paris. The medical students of Tokyo collected money and also put up a monument as a token of respect and gratitude to this patient and modest creature, the favourite subject for physiological and pharmacological investigations.

One more use of amphibians should be mentioned. Many species of frogs and salamanders are edible and serve as an excellent nutritious food. They are found in the diet of many nations, including those of Europeans, and only our food puritanism blocks their way to the counters of our food shops.

Amphibians are experimented on in research laboratories more frequently than other animals, but, strangely, very little is known of the details of their life. Research has developed in this field only during the last few decades. An attempt has been made to collect in this book data on amphibians and to illustrate their mode of life. The ecology of any species can be properly understood only against the background of Nature in general, and without such knowledge it is entirely impossible to

organize their protection, elaborate better forms of their utilization as plant defenders, introduce them into new habitats, or initiate industrial breeding. Hence, beside a description of the different frogs and salamanders of the Soviet Union, the reader will find here information on tropical amphibians which have been little discussed in the literature. Information on these creatures is important not only for a more profound understanding of amphibian biology. Some of them, evidently, will appear soon in cultures, as it has occurred with the axolotl (*Ambystoma*), the Spanish newt (*Triturus boscai*), the clawed toad (*Xenopus laevis*), and some other amphibians.

Man is obliged to ensure safe existence of the amphibians on our planet and their optimal utilization for the welfare of mankind.

The Pioneers of Continents

When the sun warms the soil in early spring and melts away the ice, one can see toads, frogs, newts and salamanders, their spawn or tadpoles in any water, whether it is a tiny pond covered with scum, or the backwater of a deep river, a large lake, a tiny brook, or even a road-side ditch filled by the spring floods.

These animals are always cold to the touch, with a smooth slimy skin and quite unlike each other. They are some of the most interesting representatives of the class of vertebrates, called amphibians.

The word "amphibian" is of Greek origin and means "leading a double life". And indeed, the majority of these animals live equally well in water and on land. In spring they migrate to water. The males find mates and the latter spawn in the water. The spawn develops in the water and later the young amphibians spend their childhood in water. But, when the breeding period ends and the young

mature a little, the amphibians begin to show an interest in the land. They refuse to be confined to the water and the majority of them abandon their birth place and go ashore. At this time amphibians may be encountered dozens of miles away from the nearest water, even at the edges of arid steppes and deserts, where they behave as terrestrial animals.

About 3000 species of amphibians inhabit the world today, not a very large figure for a whole class of animals. In turn, the class of amphibians is divided into three specific orders, and the representatives of one order are so unlike those of the other, that it is hard to guess their relationship. The most numerous order, comprising above 75 per cent of all the amphibians, is that of the tailless or hopping amphibians (anurans). They include the common frogs and toads. The specific feature of the members of this order is their hopping locomotion, which led to one of their names (this method of locomotion is rarely seen in other vertebrates).

The second and less numerous order of amphibians are tailed animals (urodeles), who resemble lizards slightly but have a smooth, moist skin like frogs. Their name emphasizes that the members of this order have retained their tails. This order includes the familiar newts.

And finally, the smallest, very little known and least investigated order, caecilians (limbless amphibians), who are very strange animals in appearance: they lack tails and are completely limbless.

Amphibians first appeared about 300 million years ago. The humid climate of the Earth at that ancient time apparently began to suffer from occasional seasonal droughts. Plants perished and rotted en masse in the sun-warmed shallow waters. The greenish-brown water rapidly lost its oxygen. The fish had to extend their head above the surface to inhale air. However, when all the water evaporated, the fish-like creatures could not sur-

vive in the sticky mess of silt and rotting vegetation. It was necessary to go ashore and find water that had not dried up. This led to the emergence of teleosts (*Teleostei*), who had partially adapted to breathing atmospheric air and had developed paired fins that assisted them in getting ashore. They were encountered to do this apparently, because of the abundance of food, the innumerable swarms of insects who were the first to inhabit dry land. Amphibians evolved from these ancient teleosts, which is the reason for their being so similar to them in many features.

The teleosts led the way for the amphibians to land but, once there, the latter had to be pioneers in everything related to life in an atmospheric medium. Hence, it is no wonder that they resemble typical terrestrial creatures in just as many characteristics.

To move around on land amphibians grew limbs that were levers connected by spheroidal joints. This major invention was a great creative victory of Nature. The limbs were so perfect that all the vertebrates, up to the higher mammals—animals and humans, have preserved their common features unaltered. As in the case of amphibians, our limbs comprise a shoulder and a thigh, a forearm and a shin, hands with a wrist, a metacarpus and five fingers, feet with an ankle, a metatarsus and five toes.

The invention of limbs necessitated the development of a strong and complex musculature, but this was nevertheless insufficient to migrate ashore. It was necessary to learn to breathe air, and the amphibians had to develop lungs to do this. As a result, they were the first creatures to inhale the invigorating air. But despite all these acquisitions the amphibians did not totally abandoned aquatic life. Their thin and tender skin needs constant moistening. To prevent the skin from drying, the amphibians live in moist regions and return to water time and again. Besides that, the majority of amphibians reproduce only

in water. Thus, amphibians maintain firm and permanent ties with the water.

The long list of characteristics that link amphibians with their fish ancestors, and the features that transformed them into real terrestrial animals, will be continued later, but first we shall discuss separately representatives of the three orders of amphibians.

Conservatives

The amphibians who inhabited the Earth in ancient times, were of tremendous sizes. The skull of a big Carboniferous labyrinthodont exceeded one metre and the dimensions of the animal itself were quite huge. Modern urodeles are pygmies in comparison. The tiniest one, the little Mexican lungless salamander (*Plethodontidae*), hardly reaches four centimetres in length, while the largest, the giant salamander (*Megalobatrachus maximus*), a native of South China and Japan, attains a length of 150-160 centimetres and weighs 8-10 kilograms, rather like a small crocodile. Its resemblance to the latter is intensified by its quite big and sharp teeth, which are skillfully used by the animal.

Very few urodeles have survived: according to different records there are today about 300-450 species. Their native land is North America. A small number of urodeles occur in Europe, North and South-East Asia. For some unknown reason they are not found in the western regions of Asia. They occur neither in India, nor in South Iran. Africa is the home of eight hundred species of urodeles, but only 4 species of them occur on the continent and those only in the Northern coastal regions, while Australia and New Zealand lack them entirely. The only region south at the equator, where urodeles are found, is South America.

Many urodeles are restricted in their distribution to

well-defined areas and never occur in other localities. The Semirechensk salamander (*Ranodon sibiricus*) is restricted to the Jungarsk Alatau mountains, while the Caucasian salamander (*Mertensiella caucasica*) occurs only in the Caucasus. It is not rare that quite similar species are found very far from one another. The habitat of the European olm (*Proteus anguinus*) is the caves of the Yugoslavian mountains, while its sole and closest relative, the American mud puppy (*Necturus maculosus*) inhabits pure spring-fed lakes in the eastern areas of North America.

Urodeles are the least specialized order and have preserved their resemblance to their ancient ancestors—the ichthyostegas. It is not without reason that they have more in common with fishes than the representatives of other orders of amphibians. As in fish, the number of vertebrae in the urodeles varies from 36 to 98, depending on the size of the animal. Unlike frogs, they have ribs which are nevertheless different from those of terrestrial animals. These ribs are short and bifurcated at the ends, resembling greatly the ribs of fish.

The body of urodeles is elongated and spindle-like, beginning imperceptibly at the head and just as smoothly merging into the tail. The majority of these amphibians possess limbs, one or more often two pairs of the common pentadactyl type, that are intended solely for terrestrial locomotion. Climbing up littoral rocks or trees, the salamanders cling skilfully to the tiniest projections on the stones, or to the slightest roughness in the bark of trees by means of a thin, easily elastic stretching web between their toes.

The closer the species is associated with water, the less it needs the limbs. The slender salamander (*Batrachoseps attenuatus*) has tiny (8-9 mm) limbs, not used for terrestrial locomotion. The eel-like salamander (*Amphiuma means*) is characterized by 2-3 cm limbs on a body of 1 metre long. The siren (*Sirenidae*) has no hind limbs. The

number of toes is reduced to 3, 2, or sometimes even one. The toes are clawless. The Semirechensk salamander (*Ranodon sibiricus*) and the Ussuri clawed salamander (*Onychodactylus fisheri*) are among the few exceptions.

More than half of the amphibians dwell in water permanently or for a greater part of the year. The aquatic forms are excellent swimmers, but are totally helpless on land. Terrestrial salamanders are poor swimmers despite their annual return to water in order to reproduce. For example, when the crested newt (*Triturus cristatus*) starts to swim, it folds its forelimbs on its back and, by regulating the angle of inclination, uses them as a depth rudder. The tail develops translational motion. The newt flaps it at a rate of 2-12 times per second. This makes it possible for the animals to maintain a speed of 10-77 cm/s, i. e. from 300 m to 2.5 km per hour. The tail of a large animal flaps less powerfully than that of a small one. If we compare the speed of the newt with the energy spent by its tail, the discrepancy between them becomes evident. The reason lies in the inefficiency of the body shape. Despite the fact that the newt's neck is hardly noticeable, this is the spot where the water boundary layer forms vortices that run along the length of the body. A substantial amount of energy is lost on the formation of these vortices.

Typically terrestrial salamanders are considered the most capable pedestrians among the amphibians. Many of them, for example, lizards, run, climb up trees and rocks. Some have a strong tail, which they use to suspend themselves from plants. American terrestrial salamander of the species *Hydromantes platycephalus* and their close relatives climb up rocks, using their tail as a fifth leg. Before lifting its hind limb from a rock, the salamander bends its tail into an arc and rests its tip behind the limb. The animals use this method for climbing up sheer walls.

Salamanders are characterized by a hopping locomo-

tion. The length of the leaps depends on the size of the animal. When the animal is in a hurry and attempts a long leap, the first one is the longest, while each subsequent one is shorter. Some salamanders rest on their tails when leaping. By pushing off with their tails, the animals can leap from 10 to 15 cm.

Terrestrial salamanders spend the greater part of the day sheltering in moist spaces between stones, rotting stumps, empty burrows.

Urodeles are not adapted for long journeys. They are sedentary creatures, pursue a settled way of life and are strongly attached to their home. The Oregon woodland salamander (*Plethodon glutinosus*) permanently inhabits the same site and leaves it for a maximum distance of 9 metres in the course of a whole year. Young animals never go so far.

The individual site may be quite big or very small. The "estate" of the bistripped salamander (*Eurycea bislineata*) is about 14 sq. m, but the animal uses it very little, rarely hunting more than a metre away from its shelter, where it hides in the daytime. The plot of the dusky salamander (*Desmognathus fuscus*) is 10 times smaller, i. e. only about 1.5 sq. m.

When it is not the breeding season, the animals are not gregarious and generally avoid shared shelters. Nevertheless, salamanders sometimes spend the winter in companies, digging into the soil, in deep burrows, rotting stumps, or at the bottom of pools.

The aquatic animals have retained gills for breathing. The gills are special outgrowths of the body. They may be located externally or hidden in cavities and have rich system of blood vessels and thin lamellae, which facilitate gas exchange between the water and the blood. When abandoning the aquatic medium, the amphibians had to learn to extract oxygen from atmospheric air. At first it seems that it would not have been a difficult task

as a litre of air contains 210 cu. cm of oxygen, whereas only a maximum of 10 cu. cm of oxygen is dissolved in a litre of water. However, it is impossible to use gills for breathing air because they dry very rapidly, so rendering gas exchange and stopping blood circulation.

For terrestrial life amphibians needed special devices located inside the body. The lungs of primitive amphibians were in the form of simple paired sacs, still characteristic of some primitive salamanders. It is not a very complicated problem to keep the walls of these internal cavities moist.

However, such primitive lungs are unable to supply the organism with a sufficient amount of oxygen. Their mechanical pumping system is not very effective. For example, air is pumped into the lungs of the three-toed salamander (*Amphiuma tridactylum*) by the coordinated movements of the floor of the oral cavity and the cheeks. The capacity of this pump is so small that the pressure in the lungs is never greater than atmospheric air pressure. Expiration is performed by efforts of the body musculature and contraction of the muscle cells in the walls of the lungs, which does slightly increase the pressure therein.

Adult amphibians generally have no gills. Only the siren, olm, blind salamander (*Typhlomolge rathbuni*), and some other primitive species retain gills or gill slits as a recollection of their aquatic ancestry. The skin is the second for all the other animals. That is why it is necessary for the amphibians to keep it wet. As well, oxygen can be absorbed by the mucous membrane in the mouth. This is useful both in water and on land.

The part played by the skin in respiration varies in different species. The thicker and rougher the skin of the animal, the more difficult it is for oxygen to penetrate it. The hellbender (*Cryptobranchus alleghaniensis*), which is quite a big amphibian, has sufficiently large lungs but they are poorly furnished with blood vessels. The hell-

bender hardly ever uses its lungs as it inhabits small and fast brooks and small rivers where the water is always sufficiently oxygenated. This animal uses its lungs rather for a hydrostatic function, like a swim bladder in a fish. The numerous skin folds, suspended from the massive limbs and highly flattened body, contribute to oxygen absorption. These parts are rich in a superficial blood capillaries. The hellbender continuously vibrates its tail and body to prevent stagnation of the surrounding water and to ensure its high degree of oxygenation. The animal survives in constant motion. But it is unnecessary for this defenseless giant to venture above the water surface and be permanently subjected to the risk of attracting some predator's attention.

The three-toed salamander (*Amphiuma tridactylum*) is not a dwarf among amphibians. Its thin and slender body reaches a length of one metre. The animal has lungs though it can stay underwater for a long time, breathing the oxygen dissolved in the water. However, it consumes the entire reserve of oxygen, stored in its lungs, after one hour underwater. The eel-like salamander (*Amphiuma means*) has elongated lungs with numerous septa and a rich system of blood vessels. The lungs are ventilated when the animal surfaces and supply only 5-8 per cent of oxygen in cold water but almost fully remove the gaseous carbon dioxide from the organism. When the water temperature goes up to 25°C, the salamander receives more than half of the required dose of oxygen by means of its lungs. The animal can survive without air only in cold and fully oxygenated water.

The mud puppy (*Necturus maculosus*) is much smaller than the animals discussed earlier. The length of the largest ones is about 40 cm. However, the mud puppy depends not only on dermal respiration. It possesses three pairs of external featherlike gills and rather underdeveloped lungs. Nevertheless, it would have been hard

for the mud puppy to survive without the latter as they supply the animal with 20 per cent of its oxygen. The big siren (*Siren lacertina*) has tiny external gills and large lungs which reach $\frac{2}{3}$ of the body length and possess numerous septa that increase the total internal surface area four times. The animal continuously sucks in air: the lungs provide the siren with 50-75 per cent of its oxygen needs, while the gills add a maximum of 18 per cent under the most favourable conditions.

The spotted (*Triturus vulgaris*) and crested (*Triturus cristatus*) newts are unable to stay underwater for a long time and surface intermittently to inhale air. The former surfaces once every 6 minutes and the latter—once in 15 minutes. Respiration becomes difficult for them during the breeding season and additional respiratory organs develop in the form of crests. Nature created the latter neither for the sake of beauty, nor for the sole purpose of attracting females. The crest contains a rich system of blood vessels and considerably increases the part played by dermal respiration.

Aquatic species of urodeles are more economic in consuming oxygen than terrestrial ones. The clawed salamander (*Onychodactylus fisheri*), which spends all its life in cold mountain streams rich in oxygen, has lost its lungs and breathes only through its skin. The fire (*Salamandra salamandra*) and black Alpine (*Salamandra atra*) salamanders, which possess quite large lungs (compared to other tailed amphibians), never use them because they live in aquatic conditions and are satisfied by the oxygen dissolved in the water. They breathe this oxygen in through their skin and the mucous membrane of their mouths.)

Lungless salamanders (*Desmognathus*), which constitute the most numerous family of urodeles, use only dermal respiration. The lack of lungs is a feature of aquatic life but many lungless salamanders have abandoned all

ties with water: they receive 83-93 per cent of their oxygen needs through the skin and remove 82-95 per cent of carbon dioxide in the same way. The rest goes through the mucous membrane of the floor of the oral cavity. When the animals move around very actively, they make up the insufficiency of oxygen by the throat, increasing its part in gas exchange up to 15-25 per cent. Salamanders with lungs receive only 32-68 per cent of oxygen through dermal respiration, but the carbon dioxide is expelled mainly through the skin.

Terrestrial amphibians possess a feature which enables them to endure an insufficiency of oxygen when high loads occur. Without it, the rather imperfect methods of extracting oxygen could not satisfy the essential requirements of the animals, would prevent active hunting and safe escape from dangerous predators. When the load increases, the oxidizing processes in the amphibian's organism never continue to the end but stop at the formation of lactic acid. This anaerobic process is performed by the splitting out of hydrogen and not by the addition of oxygen, i. e. it is effected without oxygen coming in from the outside. Later, when everything is calm, the deficit of oxygen must be completely recovered. The slender salamander (*Batrachoseps attenuatus*) needs about an hour of intensive breathing through the lungs and skin to do it.

The animal's mode of life is directly dependent on this anaerobic capacity. If it is great, the animal can run away from its enemy, but if it is small, it has to hide, to acquire poison glands or an offensive odour. This ability is useless in water because there it is impossible to recover the oxygen deficit sufficiently quickly.

The life of urodeles is most closely dependent on the availability of moisture. The majority are not adapted to life in arid areas far from water. Their requirements of water are so great that during dry weather the terrestrial species stop all activities and will not leave their shelters

in the moist underlayer in the woods, under stones, or in deep burrows. Any considerable water losses must be rapidly recovered. To this end it is best to dive into nearby water or to find at least a moist plot of soil and, pressing the belly to it, absorb moisture from it like blotting paper. Newts and salamanders suck in moisture through their skin. They possess rib grooves on the sides, which are tiny depressions in the skin that function like capillary pumps. These depressions are designed to transport water from the side of the abdomen to the back and sides for their uniform humidification.

Aquatic salamanders suffer the most when the water bodies dry up. Only a few of them have adapted to meet this calamity. The elongated dwarf siren (*Siren intermedia*) digs into the littoral soil and forms a mucous cocoon that covers its entire body except the mouth. When it dries, the cocoon protects the animal against further dehydration. Only well-fed animals survive a drought because a fifth part of their mass is fat. They metabolize it during hibernation and utilize the water that forms during fat oxidation. The dormant state may continue for more than a year but even the largest animals lose a quarter of their mass during the first 4 months, while small ones lose half of it in 12-14 weeks and sometimes perish.

Urodeles can live only in fresh water. Only the slender (*Batrachoseps attenuatus*), giant slender (*Batrachoseps major*) and some lungless (*Plethodontidae*) salamanders have adapted to life in slightly saline water. They use the lacrimal gland, as do reptiles and birds, to remove excessive salt from the organism. This gland is found in our newts in the upper rear corner of the eye socket.

The amphibian's body temperature fluctuates with that of the environment. This property has certain advantages. Owing to the fact that they do not constantly need to spend energy to maintain their body temperature at a

certain level, amphibians may be of small size, quite small mass and with an elongated body. This is entirely impossible for warm-blooded animals, even for tropical ones, because the latter shape increases greatly the ratio of the body surface area to its volume, and, consequently, the heat losses increase sharply. The struggle against such losses would require too much energy.

However, it would be erroneous to think that the temperature of the amphibian's body passively follows that of its environment. Amphibians warm themselves up by turning their sides to the sun, or by moving around actively. Hence, the Alpine salamander (*Salamandra atra*) and some of its relatives, which dwell under most severe climatic conditions, have a black or at least a dark-coloured skin. However, body heat obtained from the rays of the sun is rapidly lost in cold water. Thus, the body temperature of the eel-like amphiuma (*Amphiuma means*) is never more than 0.1°C above the temperature of the water. The preheated body of the mud puppy (*Necturus maculosus*) cools by 2°C per minute. It takes only 3 minutes for animals, moved from water at 28°C to water cooler by 6°C , to equalize their body temperature with that of the water. Mud puppies lose about 70 per cent of heat through heat conductivity and the rest of the heat is removed from inside the animal by the blood circulation.

The most reliable method of warming up in this case is to find a warm spot in the water. The tiger salamander (*Ambystoma tigrinum*) searches for water where the temperature is $18\text{--}24^{\circ}\text{C}$ and never swim into water that heats up to 27°C . Its larvae prefer warmer spots with a temperature of $23\text{--}26^{\circ}\text{C}$. In Sardinia the flat-head Alpine salamander (*Euproctus platycephalus*) and its larvae can live under temperature conditions of $20\text{ to }28^{\circ}\text{C}$, but for their habitat they choose water where the temperature remains at $22\text{--}24^{\circ}\text{C}$.

Salamanders and newts stay ashore for the greater part

of the year and more frequently encounter the danger of overheating. When it becomes too hot, the animals seek shelter under stones or in deep burrows. If the air is not very humid, they find salvation in skin evaporation, which enables them to maintain their body temperature at a lower level than the ambient. On the other hand, Northern urodeles strive to reduce body surface evaporation so as not to feel cold very much at least in warm weather. They utilize evaporation only when the air temperature rises to 30°C.

Overheating is more dangerous for amphibians than cooling. The spotted salamander (*Ambystoma maculatum*), whose habitat is in quite a warm zone, perishes at only 35.5°C. Urodeles, that have not adapted to habitats of reduced humidity, where the cooling mechanism of evaporation operates more reliably, avoid high temperatures. When they were allowed to choose a climatic zone to their own taste in the laboratory, they always preferred a temperature 5 to 10°C cooler than that chosen by frogs and toads. It is not by mere chance that in equatorial latitudes salamanders live mainly high in the mountains where it is quite cool. And in general, mountains with their fast brooks and rivers, cool shady forests, the cold darkness of deep ravines and caves are the preferred habitats of newts and salamanders.

Many urodeles have adapted to life in extremely severe climates. The black Alpine salamander (*Salamandra atra*) may be encountered in the mountains at an altitude of 3000 metres. The spotted newt (*Triturus vulgaris*) occurs in the southern part of Karelia, and the Siberian land salamander (*Hynobius keyserlingi*) penetrates far beyond the Arctic circle and only the lack of forests prevents it from inhabiting the tundra. These salamanders and newts easily survive freezing. A land salamander, frozen into the ice, was found several years ago in the North of the Asian part of the USSR at a depth of 11 metres. When it

was carefully thawed out, the animal recovered and behaved quite normally. According to some observations, land salamanders survive cooling down to -6°C and continue their activity even at 0°C .

Urodeles are predators. Only a few of them utilize vegetable food, such as certain mushrooms, in their diet. The amphibians have small conical teeth, all directed backward, thereby assisting the newts and salamanders to hold their prey, which they swallow without chewing. The teeth wear and fall out as a result of grasping the hard chitinous carapace of insects and small crustacea, but are very soon replaced with new ones.

Hunting methods are quite monotonous and simple. Terrestrial salamanders hunt for their prey on land. Tree salamanders (*Aneides lugubris*) hunt in the bushes and the trees. When dusk is falling, groups of woodland salamanders (*Plethodon cinereus*) climb up low plants and devour nocturnal pests. They hunt mainly a prey that moves no faster than 7 cm/s. When a newt or a salamander notices a mobile object, it turns to it and, after ensuring that it resembles prey, takes off in pursuit. If the fire salamander (*Salamandra salamandra*) approaches its prey to within 3 cm, the latter will not escape, even if it stays motionless for a long time. After some hesitation the salamander will attack even motionless prey.

Many urodeles smell their prey before seizing it and attack it only if they find the smell satisfactory. Urodeles grasp their prey in water with their mouths and, after bringing it ashore, beat the clumsy prey with their long tongues.

The salamanders attack from a distance of 2-3 mm and more rarely from 5-10 mm. Closely approaching the prey, the tiger salamander (*Ambystoma tigrinum*) lifts its upper jaw and opens its mouth: its tongue, flicking forward only 3-7 mm, grasps the victim and sucks it into its mouth.

If it is a familiar prey and awakens no doubts, the hunter seizes it immediately. The hunter must be quick in fast mountain brooks because otherwise the stream will carry the prey away. It doesn't matter if a mistake has been made and there is something unedible in the hunter's mouth. The salamander will spit out the unedible food and begin to hunt again. Salamanders are never at a loss if they find themselves in a cluster of "game". It does not confuse the American red-spotted salamanders (*Nothophthalmus viridescens*) to see a number of mobile objects. Only the appearance of the prey is of importance, the character of its motion, and the distance from it. Quite naturally the closer it is, the better. The smell of the prey arouses the ardour of the hunter. However, olfactory stimuli cause no hunting reactions in amphibians in darkness, though Italian cave salamanders (*Hydromantes italicus*) are evidently an exception because at home in the cave they hunt very well in complete darkness, making use only of scent. But when they leave their caves in spring and autumn, these salamanders, just like their land brothers, begin to depend mainly on their eyes. They notice a mobile prey from afar, approach it and seize their victim with their tongues. The tongue of the Italian salamander is 3-5 cm long. It flicks out in a hundredth part of a second. Salamanders can see even a dead fly if there is a sufficient contrast between it and the background. Its excellent sense of smell enables the salamander to make sure that its eyes have not let it down and that the godsend is edible.

Urodeles hunt for certain types of food only by scent. The mud puppy (*Necturus maculosus*) frequently feeds on the roe of different fish, finding the eggs that stick to stones and aquatic plants. The smell of a mobile prey is of no interest for the olm (*Proteus anguinus*). It employs scent to find clutches of eggs of other salamanders and lost spermatophores, that it engulfs with pleasure.

The larvae of spring cave salamanders (*Gyrinophilus porphyriticus*) detect a mobile prey by perceiving the vibration it generates in the water and only partially depend on scent. An experienced hunter crawls close to the prey and then sucks it into its mouth. Sometimes the larva jumps toward the prey, but this greatly reduces the chances of success, especially when the prey is freshwater shrimps.

While the spotted newt (*Triturus vulgaris*) lives in water, its stomach is always filled to 70-90% and in autumn, on land, it is filled only to 65%. Even the meagre diet of cave salamanders comprises more than 100 species of invertebrates. The diet of large species is most diverse. The Pacific giant salamander (*Dicamptodon ensatus*), whose length is only 30 cm, will not miss opportunity to catch a lizard, a shrew or a mouse. The giant salamander will be delighted with a crayfish, a large fish, and even a water vole (*Arvicola terrestris*) or a duckling. Anything can be engulfed if it lacks spines or a poisonous sting. The Alpine salamander (*Plethodon neomexicanus*) is not scared away by burning formic acid, and ants make up a considerable part of its diet. The tadpoles of the common frog (*Rana temporaria*), European common toad (*Bufo bufo*) and other amphibians are always found in the areas where newts spawn. The crested newt (*Triturus cristatus*) devours them all indiscriminately. It will not touch only the largest ones that weigh more than one gramme, because it cannot cope with such large prey. The spotted newt rarely touches the tadpoles of toads, but never abstains from the larvae of the common frog (*Rana temporaria*).

Terrestrial salamanders and newts hunt mainly at twilight. They leave their shelter in the daytime only in very humid habitats or after a heavy rain.

As a result of their similar habits all the species of salamanders, inhabiting a common area, begin to hunt

approximately at the same time. In the American state of Ohio several species of salamanders are especially numerous, for example, yellow lungless (*Desmognatus fuscus*) and bistripped (*Eurycea bislineata*) species. They live all together, next to one another, and hunt for two hours immediately after sunset. There is no extreme competition, food is plentiful because insects are most active at this time.

Amphibians need very little food to maintain vital activity. Their digestion is very slow. The amphibian needs 4 days to digest a meal at a body temperature of 15°C, and 7 days at 12°C. Amphibians do not perish in unfavourable dry years, they simply stop growing. Sometimes they have to resort to extreme measures. Fire salamanders (*Salamandra salamandra*) leave their larvae in rain pools, that form in spring on the rocks, where is absolutely nothing edible. After some time, the grown up larvae begin to hunt their smaller brothers.

If the climate is favourable, newts and salamanders hunt all year round. The red-backed salamander (*Plethodon cinereus*) in the American state of Indiana, lives in winter in the soil at a depth of 30-75 cm, most often in anthills, where it feeds on the larvae of March flies (*Bibionidae*) and ants. Salamanders hibernate in winter in countries with a temperate climate.

Amphibians are unable to fight strong enemies. The majority have neither teeth, nor claws, or sharp fins, as do fish, or a carapace as do turtles. Only the giant salamander (*Megalobatrachus japonicus*) has teeth of a size to permit the little creature to defend itself. The sharp tips of the ribs in some salamanders protrude externally and a predator can prick itself on these. The ribs of the salamander (*Triturus waltli*) are very long. The round, button-like tiny thickened sections of skin with holes in the centre, where the thin needle-like ribs stick out, are brightly coloured. These features assist the predator to

recognize who it is dealing with. At moments of danger the salamander strikes a pose in such a manner that the ribs stick out as much as possible. This defence is reinforced by numerous poison glandules, which are spread all over the body. The poison is not strong but when it enters the fresh wounds in the mucous membrane of the predator's mouth, made by the sharp ribs, the predator will spit out its prey. It is a weak defence, but better than nothing.

Sometimes, in case of danger, terrestrial urodeles resort to cunning. In an attempt to confuse the attacker or to lead it into error, the salamanders raise either their whole body on to their feet or only the hind part, to apparently increase their size. Sometimes they coil into a ring, extend or draw in their limbs, curve their tails into an arc, or lift it upwards.

When the spotted (*Ambystoma maculatum*), Texas (*Ambystoma texanum*), mole (*Ambystoma talpoideum*) and Jefferson (*Ambystoma jeffersonianum*) salamanders see a tiny colubrid (*Colubridae*) snake they raise and coil their tail, curve their body, beat it with their head and attempt to grasp the snake with their weak mouth, simultaneously making threatening sounds. If it is all to no avail, they run away. Oedipines in this case slide away like snakes.

At the slightest touch a salamander feigns death, and can remain so for more than 20 minutes. Animals, who are clever enough to remain motionless, survive more often than those who attempt to escape.

The first reaction to danger in aquatic salamanders is to lie motionless. The mud puppy (*Necturus maculosus*) shams death and even holds its breath and arrests its heart beat. All these measures are not excessive in water. Even the weakest sounds propagate much further in water than in air. If it is a large and dangerous predator, whose size exceeds that of the salamander, it is best to run

away. The olm (*Proteus anguinus*) demonstrates in this case an enviable agility and excellent orientation in its cave. It runs away into heaps of stones, cracks or other shelter.

Some salamanders successfully use a distracting manoeuvre of their tails. A whole series of typically terrestrial salamanders, including the Caucasian salamander (*Mertensiella caucasica*), in case of danger shed their tail like lizards and, at a small cost, save their life. It is interesting to note that female lungless salamanders (*Plethodontidae*) sacrifice their tails more often than males. It is certainly not due to absent-mindedness. It is simply that during the period of reproduction they protect the spawn and are less apt to run away in case of danger than the males. The yellow lungless salamander can drive large bugs away from the spawn, and related or unrelated salamanders of similar size. They are unable to cope with large salamanders and snakes and, consequently, shed their tails.

The most efficient weapon of anurans is poison. All the newts and salamanders are poisonous to a certain extent, but some of them are really dangerous. The poison is produced in the greater paired glands behind the eyes and in the lesser glandules on the back. They extend slightly above the skin like warts. The secretion of the mucous glands also contains poison but it is weaker. Amphibians have no mechanism to discharge their poison. It is squeezed out when the skin is stretched, or when compressed between the teeth of the predator. The discharge of the glands is a viscous white fluid that smells like muscadine.

The majority of people never suspect that European newts are poisonous. And indeed, children, who bring home a jar with newts, run no risk. Their poison is not dangerous to people. But a lizard, who grasps a newt by the head, perishes very soon from respiratory paralysis

and cardiac arrest. The subcutaneous injection of the poison of a spotted newt (*Triturus vulgaris*) into a dog or a rabbit causes a rise of blood pressure, destruction of red blood cells, and the formation of thrombi. If the dose is large, paralysis occurs very soon, respiration and heart beat stop, and the experimental animal perishes. The lethal dose for warm-blooded animals is 7 mg per 1 kg of body weight.

The Californian (*Taricha torosa*), brook (*Taricha rivularis*), grained (*Taricha granulosa*), and other American newts excrete such strong poison that it would be simply unreasonable not to utilize it for defence. Instead of hiding away from predators, the more poisonous salamanders dress up in bright garments and follow a free way of life. The fancy black-and-orange colour of the Californian newt cannot be confused with anything else and the predators never touch the dandy. And if a young thoughtless heron engulfs him, it will suffer for several minutes while striving to spit the newt out. One lesson like this will last a lifetime.

The mud salamander (*Pseudotriton montanus*) possesses a strong neurotoxin and in case of danger actively shows off its orange belly.

A dangerous beauty of this kind is found also in the USSR. It is the fire salamander (*Salamandra salamandra*). Its coal-black body is covered with large, bright orange-yellow spots. A medium-sized predator, who swallows a fire salamander, will perish from its carelessness if unable to spit it out.

It is interesting to note that the representatives of only some races are poisonous in some species of salamanders. This refers, first of all, to the Jordan woodland salamanders (*Plethodon jordani*). For an unknown reason the granular glands of some animals produce a poisonous secretion, while in others it is hardly found at all. More surprising is the fact that the poisonous animals "rouge"

their cheeks, and the most dangerous ones show off in red "stockings" and "shoes". Birds, who feed on salamanders, know it very well. They touch red-cheeked animals quite rarely and never touch red-legged ones.

The American red-spotted salamander (*Nothophthalmus viridensis*), which, in accordance with its name, is dressed quite conspicuously, is entirely inedible. Pseudonewts (*Pseudotritons*) take advantage of this circumstance quite skilfully. If the red-spotted salamander lives together with the mud (*Pseudotriton montanus*) and the red mud salamanders (*Pseudotriton ruber*), these latter two harmless imposters wear red clothes, skilfully imitating their dangerous relative. The red mud salamander grows much faster under favourable conditions than its poisonous relative. The difference is so great that the predators are not confused any more, therefore the red mud salamander wears its fancy dress only during the first two or three years of its life. When it grows very big and it becomes difficult to deceive predators, it changes its red attire for a dark-brown dress and becomes very careful.

The poison of salamanders has been named salamandertoxin. It is stronger than the poison of newts and may cause spasms. The lethal dose for a dog is 0.7-0.9 mg per 1 kg of its body weight.

Very few urodeles emit sounds. The spotted salamander (*Ambystoma maculatum*) can produce two types of sounds. One type has been recorded during the mating period, while the other may be heard at any time. The meaning of these audio signals is unknown. Neither males nor females showed any response to taped reproduction of these sounds.

The Californian newt (*Taricha torosa*) produces three types of sounds with a duration of 0.1-0.4 s and a frequency of 1500-8000 c.p.s. When black Alpine salamanders (*Salamandra atra*) are held in the hands, they "talk" by single brief sounds or whole series of signals.

They can emit them with an open or closed mouths, in the air or underwater.

The slender salamanders (*Ambystoma gracile*) of West Canada make low and very brief sounds. They are produced only by adult males in the presence of their relatives. The signals are associated with aggressive-defensive behaviour. They begin to sound when hierarchic relations are being established in a group of animals and stop when the question of who is who is solved.

The way of life of urodeles is monotonous. They have very few problems: to avoid drying and overheating, to find something edible if the weather permits, to find reliable shelter for the winter, and to reproduce in the spring. That doesn't mean that newts and salamanders are hopelessly stupid creatures. Tiger salamanders (*Ambystoma tigrinum*) are easily taught to find their way in a T-shaped labyrinth. The fire salamander (*Salamandra salamandra*) memorises the topography of its hunting area very well. When returning home, it uses visual references and clearly remembers a picture hanging over the entrance to its shelter in the laboratory. Cave salamanders (*Hydromantes gormani*) can perceive a magnetic field and by its means orient themselves in the depth of their caves.

Having learned something in their infancy, newts and salamanders can utilize this knowledge as adults. These learned skills are not lost during metamorphosis, even though it is accompanied by certain changes in the brain. The animals use the experience they gain throughout their lives, and their lives are quite long. For example, the giant salamander (*Megalobatrachus japonicus*) can live for 57 years, the red-bellied Japanese salamander (*Triturus pyrrhogaster*)—for 25, the fire salamander (*Salamandra salamandra*)—up to 24, and the crested newt (*Triturus cristatus*)—up to 28 years.

Urodeles are quiet, secretive, unobtrusive creatures that we see very rarely. They demonstrate their real spirit

only during the breeding season. It is the most interesting period in the life of amphibians, and we shall speak about it separately.

The Frog Princess

The world of amphibians is an amazing one. If one sheds one's prejudices and looks at it more carefully, then the ugly frog with its cold, moist skin, protruding eyes and webbed feet is not inferior to a princess in the refinement of its movements and its exquisite attire.

Frogs have a characteristic well-known appearance. All other anurans, namely, spade-footed toads (*Pelobates*), toads (*Bombina* and *Bufo*), tree-frogs (*Hyla* and *Dendrobates*) resemble frogs in appearance but one cannot call them very close relatives.

Frogs of the genera *Hyla* and *Rana*, and toads of the genus *Bufo* are quite small creatures. It is true that the largest frog, the Goliath frog (*Rana goliath*) of the African Republic of Cameroon, reaches a length of 32-33 cm and a weight of 3.5 kg.

But these are giants; small frogs sit comfortably on a human thumb nail. The Cuban dwarf (*Sminthillus limbat*), for example, reaches barely a centimetre in length. Best-known among the little ones are the spade-footed toads (*Pelobates*) of South-East Asia, the frogs (*Brachycephalus*) of Guiana, and the South American toads (*Pseudoeurycea*), whose body length is only 15 mm. The males of terrestrial savanna frogs (*Phrynobatrachus*) in East Africa reach a length of 13 mm, while the females are 17 mm long, and the maximum size of the males of the webless leaf-frogs (*Eleutherodactylus sisypodemus*) of Jamaica is 14 mm, while the females are 18 mm long. Slightly bigger is the pumilio tree-frog (*Dendrobates pumilio*) and some frogs of the species *Hyla*.

Anurans have excellently conquered our planet thor-



Giants among toads can hardly fit on a human hand. Marine toad (*Bufo marinus*)

oughly, invading it almost to the polar borders of the continents. They occur in forests and swamps, in any freshwater bodies, in the steppes and even in the depth of deserts, if they can find there at least a tiny source of water.

Adapting to the most diverse habitats, tailed amphibians have learned to move around in water, on land and in the air. It is not surprising that they bear little resemblance to their ancestors in size and appearance. The structure of their body is quite peculiar: the big, wide head blends directly into a wide, short body. It has neither a neck, nor a tail, but instead possesses two pairs of well-developed limbs. The Australian desert toads (*Chiroleptes platicephalus*), and the tree-frogs of the spe-



Tree-frog (*Hyla arborea*)

cies *Phyllomedusa* have a thumb which is opposed to all the other fingers as in *Homo Sapiens*. Amphibians have only four fingers. Nails are not common amongst frogs *Rana* and *Hyla*. They are found only in some burrowing toads (*Rhinophrynus dorsalis*) and clawed frogs (*Xenopus laevis*).

The hind limbs are usually 1.5-3 times longer than the front ones and serve for moving around in leaps. The little creatures can walk and even run, as all other animals do, but the majority of anurans prefer to leap. If the length of the jumper is related to the distance it can cover, then the anurans will be champions among vertebrates in this sport. One of the smallest South American tree-frogs with a size of 17 mm can leap to a distance of 75 cm. The black-spotted frog (*Hyla nigromacula*) with a length of only 30 mm easily leaps to a distance of 1.5 m, while the

agile frog (*Rana dalmatina*), who inhabits Europe to the West of the Carpathian mountain system, makes 3 m leaps in case of danger! However, not all the amphibians are so capable. Many narrow-mouthed toads (*Breviceps*) can only creep. Flying frogs (*Rhacophorus*) find themselves in the most complicated situation. Each step they make is fraught with danger but at a breath-taking height they leap so easily and light-heartedly from one leaf to another that birds seem clumsy compared to them. Their virtuosity is explained by special accessories, which enable them to attach to the smooth surface of tree trunks and leaves. The finger tips of flying frogs have disks or scales that act as suction cups. Their finger tips periodically secrete a sticky fluid to ensure reliable adhesion without air leaks, and have special muscles to flatten the scales, so that they can press more tightly to the substrate. In addition, the skin on the neck and belly of the majority of flying frogs contains glandules that secrete the same sticky fluid as the scales. During locomotion the flying frogs employ two mechanisms for sticking to the substrate. The capillary forces of adhesion function only on a smooth surface. The considerable surface area of the belly in this case serves as an excellent suction cup. The flying frogs hold on to rough surfaces mainly by their feet. Adhesion is possible by the sufficient matching of the finger scales to the texture of the surface, i. e. by matching the bulges on the finger tips with minute depressions on the substrate. This enables them to stick to the surface of a leaf with the entire bottom side of the body and move freely in the vertical plane even on wet glass. Suction cups are also used successfully by aquatic amphibians. The Japanese flying frog (*Rhacophorus buergeri*) uses them to hold on to stones in fast mountain streams.

Leaf-frogs of the genus *Phyllomedusae* have real grasping toes. The first digit on their fore and hind limbs is



The discs on the finger tips and belly of Australian tree-frog are an excellent mechanism for sticking to the substrate

opposed to the others. They climb up to great heights but are very slow, just like sloths and chameleons. These skinny creatures are unable to leap or swim.

Anurans propel themselves in water by rapid jerks of their hind limbs, which have swimming webs between the toes. The forelimbs are not used for swimming and frogs simply clamp them to their bodies so that they do not hinder their swimming. The swimming style, used by amphibians, is quite efficient, which is why it is the basis of such sport styles as breast stroke and butterfly stroke, while the design of the frog's limbs has been used in developing flippers.



The suction cups on the fingers of Australian Litoria hold it tight on stones in fast streams

Asian flying frogs (*Rhacophorus*) have learned to fly, or, to be more exact, to glide from one tree to another, just like flying squirrels. Flying frogs have extremely long digits on the fore and hind limbs with a web between, which is not for swimming but for flying. It is supplemented by the skin edges of the forearms and the extended digits. The frog inflates its body before leaping and, taking off from the substrate, spreads its limbs and digits as much as possible. It covers easily a distance of 10-12 m by using the extensive area of its webs.

Those frogs, which spend the greater part of their life on land, have also needed to develop special accessories. Narrow-mouthed (*Breviceps*) and spade-footed (*Scaphiopus*) toads dig burrows with their hind limbs. The shortened shin and the strongly developed calcaneal tuber equipped with a hard corn are used as a spade. Working

with the right and left legs in turn, forcibly straightening them and turning them slightly sideways, the animals use the calcanean tuber to dig out and then throw away the earth. Some diggers use their forelimbs, while the narrow-mouthed tree-frog (*Microhyla*) digs the earth out with its snout. The bones of the shoulder girdle are fused firmly together, so that the head may be used as a ram.

The body of anurans is covered with naked and totally unprotected skin. The paradoxical hairy frog (*Astylosternus robustus*), found for the first time in Gabon in 1900 (Central Africa), is an exception. The thighs and sides of this frog are covered with thick hair. Their discovery caused a great sensation. However, the puzzle was soon solved. On close examination the "hair" turned out to be only long, thin outgrowths of the skin.

Amphibians need moisture for their normal existence. The frog's skin is always covered with mucus, which is produced by numerous glands in the skin. The mucus dries up rapidly in warm and dry weather and the glands of the skin must work quite intensively. Unlike other higher animals, the skin of the frog is not attached all over the whole body, but only in certain spots. The subcutaneous space contains a small amount of lymph. This reserve of moisture is also used for the production of mucus.

A liquid mucous film, limiting further evaporation, forms on the skin of frogs and toads who bask in the sun. It is most important for tropical amphibians to reduce evaporation. The secretion of the glands in the skin of leaf-frogs (*Phyllomedusa*) contains fatty inclusions. When scratching itself, the frog smears the fat all over its skin and this lubricant reduces moisture loss.

As has been mentioned earlier, the permanently moist skin of amphibians, covered with mucus, is perfect soil for the development of all kinds of microorganisms. Frogs and toads actively defend themselves against these

by means of poisons. The mucus, secreted by glands in the skin, contains bactericidal (bacteria-killing) and bacteriostatic (inhibiting the reproduction of bacteria) substances. This property of the frog's skin is widely known and has even found practical application. Peasants in summer put a frog into a milk can, so that the milk does not sour for a longer time. The poisonous mucus of the skin inhibits the reproduction of lactic-acid bacteria and the milk is preserved very well indeed.

The poison of most of our amphibians is entirely harmless for humans. But even in this case Nature has not stopped halfway. The skin glands of many tropical frogs secrete such strong poison that it is dangerous even to large animals, and makes an excellent means of defence. It is true that, unlike the majority of poisonous creatures, frogs lack any specialized mechanism such as teeth or spines for injecting the poison directly into the blood stream of the attacker, and the skin and mucous membrane are considerable obstacles to penetration into the organism. For this reason, the poison must be very strong. Incidentally, it is not snakes but amphibians who produce the strongest poisons. The champion is an inhabitant of the tropical forests in Colombia, the tiny so-called cocoa frog, whose size is only 2-3 cm. Its skin mucus is so poisonous that a mere touch may be lethal for a man. Indians use the skin of these frogs to poison their arrows. To do this they string the frogs on a stick and hang them up over a fire in order to evaporate the poisonous substances, which they smear on their arrow points. The poison of one frog is sufficient to make 50 poisoned arrows. An animal, hit by such an arrow, perishes immediately.

Scientists have only recently found a large tree-climbing frog in South America, which the Indians of two local tribes have long used to poison their hunting and war arrows. The frog was so poisonous that it has been

named the terrible frog (*Phyllobates terribilis*). Even 2 μ g of its purified poison can kill a man. The process of making poisoned arrows is very simple. It is enough to rub the arrow's tip against the frog's skin and then dry it well. The poison is stable and preserves its strength for several years. Despite this terrible weapon, the frog has an enemy – a small snake that is fond of feeding on the young of this species.

However, it is not essential to possess such a lethal weapon. The giant tree-frog (*Hyla vasta*) of Haiti has a body colouration that resembles the bark of trees, where it lives as a rule. Its dermal secretion causes a burning sensation on the human skin like that caused by fresh nettles. Another frog, the Brazilian flying frog (*Rhacophorus*) secretes a thick caustic liquid and even the most indiscriminating predators spit it out in disgust.

The most poisonous amphibians in the USSR are toads (*Bombina*). Their poison produces an offensive odour, which stimulates the secretion of tears, and, if it comes into contact with the skin, burning and pain. Any predator, who has once eaten a toad, will never do it again. The poison of the variable toad's (*Bufo viridis*) large glands, arranged where the neck ought to be, has been thoroughly investigated.

The alveoli of the small poisonous glandules open freely on the skin surface. A frightened toad discharges tiny drops of poison from all the glandules simultaneously and becomes inedible for the predator. If the latter still grasps it, then it may express some poison from the large glands. The poison will not spill out by itself, because the ducts of the alveoli are closed with a plug of stratified epithelium. The discharge of the second portion of poison frequently saves the toad's life.

The European midwife toad (*Alytes obstetricans*) produces quite a strong poison. It causes irritation of the mucous membrane in the upper respiratory tract, acting



The European common toad (*Bufo bufo*) has large glands that contain poison

as a tear gas. The poison of some local species of toads is used in the Argentine to cure toothache. The skin mucus of the animals sometimes produces an excellent analgetic effect if it is applied to the gum near the aching tooth. However, this method of treatment may lead to tragedy: cases of lethal intoxication with the poison of this toad have been recorded. The poison of the South American wood frog (*Dendrobates tinctorias*) causes only itching of the skin, if handled, but it kills even a large animal rapidly when injected.

Before reaching the end of the story about the skin of the amphibians, we should mention that they are frequently very brightly coloured, especially those who live in the tropics. Whereas our northern species have a bright belly, the southern ones are distinguished by their bright

back, which is coloured in shades of yellow, orange, violet and red. The purpose of the bright colouration is to attract attention. The majority of these frogs are very poisonous. Predators easily distinguish them from non-poisonous animals and never touch them.

Many poisonous frogs are exceptionally beautiful. Most attractive among the African beauties are the bi-striped frogs (*Phrynomantis bifasciata*), whose skin is all shades of gray with two reddish-pink stripes along the back, a spot of the same colour on the sacrum and small spots on the legs. The frog is very slow, clumsy, and, unlike the majority of amphibians, follows a diurnal mode of life and hides at night. If someone carelessly touches it, the frog secretes a white sticky fluid, which it is difficult to get rid of. It causes burning and later widespread inflammation of the skin. It affects a wide area that has not even been in contact with the poison.

The cloud-forest frog (*Atelopus stelzneri*) is beautiful and poisonous. The frog's back is bright-violet, while the belly and the toes are red. It is never touched by birds, snakes or other predators. Assured of its immunity, the violet-coloured frog slowly creeps about in bright daylight over the uninhabited sandy hills. The tree-climbing frog (*Dendrobates occultator*) has a red back and yellow spots on the sides, while the tree-frog (*Dendrobates lehmani*) is covered with black skin with bright yellow stripes. Both of them are quite noisy creatures, constantly emitting humming and twittering sounds. No predators would wish to feed on them. The spotted tree-frog (*Dendrobates tinctorius*) is also brightly coloured. It is dark-brown, sometimes almost black, and covered with white, yellow, red and light-blue spots. Just like the majority of poisonous frogs, the spotted tree-frog is slow and follows a diurnal way of life. The Indians of Colombia used its skin secretion to make poison for their arrows, when they hunted monkeys and birds.

The general rule that bright-coloured amphibians are always poisonous, has certain exceptions. An interesting creature, known to the local population as the tomato-frog (*Dyscophys antongili*) inhabits the Madagascar. Its body, head and toes are bright-red and only its belly is white. The females are very brightly coloured, but these animals are not poisonous. The skin secretion of the tomato-frog is harmful only to microorganisms.

There are certain specific varieties among the poisonous frogs, whose body is coloured in common dark-green shades, and the patterned skin assists them in hiding. It hides in daytime but if a predator still discovers it, it tries to warn its enemy that it is inedible. This is the way the fire-bellied toad (*Bombina bombina*) behaves. Its back is brown-gray or black with dark spots, and its belly and some parts of its legs are bright-yellow. At a moment of danger the toad bends its back, turns its head up, twists its limbs unnaturally, and in general, does everything to show its brightly coloured belly. It may even turn over on its back. Any grass snake, which takes this toad into its mouth, will never do so again.

The Venezuelan horned toad (*Ceratophrys cornuta*) when attacked inflates its body to an impressive size and emits loud abrupt shrieks. At the moment of danger the marine toad (*Bufo marinus*) flattens its body against the ground and inflates itself. Any dog, who carelessly grabs a marine toad, may lose its life. The Siam bull frog (*Calula pulchra*) inflates itself so strongly that it becomes ball-shaped, its wrinkled skin stretches and two wide yellow stripes appear on its back.

The majority of anurans possess camouflage colouring, which assists them in hiding. This colouration sometimes imitates a particular pattern. The slender tree-frog (*Hyla crepitans*) resembles a fading leaf, while the geographical tree-frog (*Hyla geographica*) looks like a dry leaf. The black-spotted tree-frog (*Hyla nigromaculata*) is remini-



Australian tree-frogs remain inconspicuous in the bright green of growing vegetation because of their cryptic colouration

scent of tree bark covered with lichen. The warty skin of the tree-frog (*Hyla giesleri*) resembles a lichen knot on a tree trunk, while some flying frogs (*Rhacophorus*) look like fungus-infected green leaves.

The "clothes" of anurans possess a surprising property: their colour can change very rapidly. The banana frog (*Magolixalus laevis*) is chocolate-brown in the daytime and red-brown with pearl spots by night. It is important for frogs that do not hide, and who spend the whole day in the open, attached to some object, not to differ from the surrounding background. It is not fortuitous that the colour of a tree-frog (*Hyla arborea*), sitting on a leaf, corresponds exactly to the colour of the latter. The frog will be light-green on light-green leaves, dark on dark leaves, and almost black on a dark dry branch. Tree-frogs possess the richest range of colours. The most



Cryptic colouration makes the European common toad inconspicuous on the soil's surface

talented “painters” are tree-frogs (*Hyla*) in Trinidad and frogs of the genus *Phrynobatrachus* in Cameroon. Their colouration includes white, yellow, orange, brick-red, brown, chestnut, purple, pink-violet, pink, bright blue, and green colours. Amphibians change their appearance for camouflage, but during the nuptial period they try to be conspicuous to their partners.

There is nothing mysterious in this change of colour. The skin of the amphibians contains special arborescent cells, chromatophores, that have a small body and thickly branching outgrowths. The pigment granules are inside the cell. The black pigment, melatonin, is encountered more often than others. Amphibians also possess chromatophores with red, yellow and blue-green pigment, as well as light-reflecting plates. If the granules of pigment

are collected into a tiny ball, they have practically no effect on the colour of the animal's skin. But when the pigment is distributed uniformly across all the outgrowths of the chromatophore, the skin acquires that particular colour. One animal may possess chromatophores, containing pigments of several colours. In this case each type of chromatophores is arranged in a separate layer in the skin. By the simultaneous use of several types of chromatophores, amphibians can decorate themselves in several colours. In disk-tongued frogs (*Discoglossus*), the xanthophores, containing yellow pigment, are closest to the skin surface. A layer of iridophores with green-blue pigment is arranged beneath them, and melanophores are found still deeper. The outgrowths of the latter are interwoven among the iridophores. When the frog is on a light background, the melanin is collected in clots and hidden behind the iridophores. Different combinations of the yellow and blue-green colours determine the colouration of the frog. When the background is dark, the black pigment fills the outgrowths of the melanophores, covering the iridophores completely, and the frog turns dark. The plates, making up the light-reflecting layer, add an iridescent pearl brightness to the skin.

Special hormones control the chromatophores. One of them, the pigment-stimulating hormone, distributes the pigment uniformly across all the outgrowths of the chromatophore, while another, the pigment-concentrating hormone, gathers them into one compact ball. The colour of the animals also depends on the temperature and humidity of the air. The skin darkens in cold weather and becomes brighter when it is hot. Amphibians maintain their body temperature at a favourable level by means of the chromatophores. It is well known, dark shades absorb the sun's rays best and assist the animals to warm in cold weather, while a change to light colouration in hot

weather prevents overheating and avoids the need for intensive evaporation of water, which ought to be conserved at this time. Colour may change also from the effect of great excitement. The ability of frogs and tree-frogs to change their skin colour to match exactly the colour of the surroundings is most surprising. It is closely associated with visual function, and, therefore, it will be necessary to return to these mechanisms, when dealing with the problems of vision.

There is an assumption that the most capable amphibians can change their colouration by memory, using information from receptors other than visual ones. Experiments on tree-frogs have indicated that information from the tactile receptors of the belly and legs is highly important to them. Blind animals, placed on the rough surface of large-grain abrasive paper, turned brown-black, evidently trying to adjust the colour of their bodies to the colour of a tree trunk, which was invisible to them but where they seemed to be sitting. When they were placed on a smooth surface of the same colour, the tree-frogs turned green, as if they were sitting on the bright green surface of a tree leaf.

As they control the colouration of their bodies by means of hormones, produced and secreted into the blood in small quantities, amphibians are unable to change their colour instantaneously: they need a day and night to do it. Only a few of them can change colour in an hour, as a rule, optimum air temperature is required for this.

The pigment is synthesized by the chromatophores proper. If the pigment is distributed across the whole cell, which means that it is used intensively, the chromatophores, undertake intensive synthesis of the dyestuff. And, on the contrary, when pigment is gathered into a clot and unused for a long time, it is slowly destroyed. If clawed toads (*Xenopus laevis*) are kept for six months on

white soil, it takes several weeks for their skin to darken again. The unwanted pigment is totally destroyed during those six months.

The body growth of anurans is accompanied by periodic shedding of the skin. Our edible frogs (*Rana ridibunda*) do it four times a year. The skin peels first from the legs, then from the body, and finally from the head. The frog eats up the shed skin and so saves itself the necessity of synthesizing the skin pigment again.

Anurans have not evolved new methods of extracting oxygen. They breathe by means of lungs that are more efficient than those of their tailed relatives, owing to the cellular structure of the walls. Oxygenation of the blood begins in the oral and pharyngeal cavities, which contain an abundant supply of blood vessels. Due to their lack of rib cage, anurans are unable to suck air into the lungs by expanding the chest, as do all other vertebrates. The frogs have to pump in the air. Respiration begins with the opening of the nostrils and depression of the floor of the mouth, whereby the air is sucked into the oral cavity. Then the nostrils are closed by valves, the larynx opens, the floor of the oral cavity lifts and discharges the air into the lungs. The capacity of the pump depends on its size. The wider the mouth, the greater the volume of air pumped into the lungs at each breathing movement. Expiration is effected by contraction of the abdominal muscles and deflation of the lungs.

Unlike mammals, whose internal surface area of the lungs (total surface area of the lung alveoli) is 50-100 times greater than the surface area of the skin, these areas are almost similar in frogs, and, therefore, dermal respiration is of great significance. Our edible frog (*Rana esculenta*), even in the open air, receives most of its oxygen through the skin and releases through it almost all its total carbon dioxide.

When the frog submerges, the skin takes over all the



The wet skin of many Australian Litoria acts as an additional respiratory organ

breathing function, and it is difficult for the frog if the oxygen concentration in the water is low. In this case some of them begin to think of gills, such as the fine hair-like papillae that grow on the skin of the male hairy frogs (*Astylosternus robustus*) during the mating period, and are used for extracting oxygen from the water. Finding a female is hard work and the males would suffer greatly from an acute oxygen deficit if it were not for the “hairs”.

The clawed toad (*Xenopus laevis*) lives in water but breathes mainly with its lungs, which supply more than a half of its oxygen needs. The toad surfaces regularly for fresh air. All the frogs and toads sharply reduce their

metabolism on submerging, because otherwise they would not have enough oxygen. The large marine toad (*Bufo marinus*) reduces consumption by half when in the water and yet is still unable to stay underwater for more than 16 hours. It usually ventilates its lungs 2 to 6 times an hour.

Lungs create certain difficulties for underwater life. When they are inflated, it is impossible to stay on the bottom. Hence, the clawed toad compresses them and, increasing intrapulmonary pressure, reduces the volume of its air cavities.

Toads sometimes change to dermal respiration without submerging. Spade-footed toads (*Scaphiopus*) spend the greater part of their lives burrowed into the earth. They ventilate their lungs on the surface by moving the floor of the oral cavity and inflating the sides. These respiratory movements of the toad stop an hour after burrowing into the earth and the animal changes over completely to dermal respiration.

If necessary, frogs and toads, like urodeles can successfully employ aerobic metabolism. The leopard frog (*Rana pipiens*) can survive for 5-7 days in cold water totally deprived of oxygen, by means of aerobic glycolysis and the accumulation of an enormous amount of lactic acid in the organism by 50-60 times the normal level. The amount of oxygen available in this way is insufficient for the majority of amphibians, when they move around actively. The amount of lactic acid in the blood of a royal tree-frog (*Hyla regilla*) is so great after a short time hunting, that the animal needs 1-1.5 hours of rest to replace its oxygen deficit.

The cardiovascular system in frogs is more efficient than in urodeles. They have a three-chambered heart with two auricles, connected with the single ventricle by a common orifice. The greater skin arteries are separated from those of the lung just before the latter enter the

lungs. The close connection of the skin and lung arteries is not accidental, their function is identical: they carry blood to the organs from which it receives oxygen.

The frog's heart works quite rapidly. It performs 10-20 contractions per minute in cold weather, at 24°C the pulse rate increases to 50-70, and up to 100-115 beats per minute in the fire-bellied toad (*Bombina variegata*) and the tree-frog (*Hyla arborea*). The blood pressure in these species reaches 30-38 mm Hg. This figure is quite high for such tiny creatures as frogs and toads. High pressure is necessary to move the erythrocytes through the fine capillaries. The size of the erythrocytes in frogs exceeds that of humans by 7.5 times.

The digestive system of amphibians is quite primitive. It comprises a pharynx, a short gullet, which widens and gradually turns into a stomach and then into an intestine. The liver with its gallbladder, and the pancreas are well developed. Compared with fishes, only the salivary glands represent a principally new organ. Their utilization is a characteristic feature of terrestrial animals. In the case of amphibians they secrete only water and a small amount of mucous for wetting the food. The saliva contains no digestive enzymes and does not directly participate in the process of digestion.

Swallowing action is quite unusual in amphibians. When the food enters the frog's mouth, certain muscles retract the eyeballs so deeply into the oral cavity, that they force the food into the pharynx. The devices of Nature are indeed inexhaustible!

All adult anurans are predators. They hunt their prey in water and on land, catch it on plants, and some amphibians even manage to snap up flying prey. Flying frogs (*Rhacophorus*) snap up their prey almost like birds. The basic tool for getting food is the tongue. It is attached in the mouth not by its rear end, as in all other animals, but by its front tip. When a frog sees a creeping

fly, it flicks its tongue at the prey. The tongue hits and stuns the prey, which adheres to it, and the frog pulls its tongue in just as rapidly. It takes only a moment for the prey to disappear. It all happens so quickly that it cannot be observed by the human eye. This system operates only in the air. Aquatic animals have no tongue. They grasp their prey with the mouth and the forelimbs assist in holding it.

Amphibians feed on worms, mollusks, insects, crustaceans, and large species even engulf some vertebrates: fishes, rodents, birds and their own brothers amphibians. Fastidious feeders are found only in the tropics, where there is an abundance of food. The crab-eating frog (*Rana cancrivora*) feeds only on crabs. The green and black poison frog (*Dendrobates auratus*) snaps only at little flies, tree-frogs (*Brachycephalidae*) feed on aphids and mosquitoes, the smith frog (*Hyla faber*) feeds on nocturnal moths, and the panther frog (*Rana pipiens*)—on ants. The burrowing toad (*Rhinophrynus dorsalis*) eats only termites, licking them away with its extremely mobile tongue. The “gourmands” narrow-mouthed toads (*Brevicipitidae*) eat termites and live in the termitaria. The presence of dangerous insects has forced the animals to develop special measures of defence. The narrow-mouthed toads, like ancient knights, wear armour. Their skin glands produce an abundant gluey secretion, which turns rapidly into a hard crust, and their eyes are surrounded by a bone ring.

The European common toad (*Bufo bufo*) in the southern regions of our country hunts hundreds of species of invertebrates and never hesitates to vary its diet with something new, as long as the victim is mobile and its size appropriates. The diet of the terrestrial frog (*Rana terrestris*) in Siberia includes 70 items. The diet of amphibians is made up of whatever is in greater abundance, which doesn't mean that it has a better taste.



The common toad in the Caucasus (*Bufo bufo verrucosissima*) is extremely gluttonous and frequently attacks prey that is hardly smaller in size

The larger the frogs, the more commonly do they feed on their own kind. In July they devour tadpoles and then young frogs. The density of edible frogs (*Rana ridibunda*) at this time near the banks of water bodies may reach as much as 100 per square metre. Only a few adult frogs are found in this assembly. Hence, it is of no surprise that the part played in their diet by younger frogs increases sharply.

Frogs eat a lot. The bull frog (*Rana catesbeiana*) is satiated only when the weight of the food in the stomach reaches 10-35 per cent of its body weight.

The Australian white tree-frog (*Hyla coerulea*) is extremely gluttonous. The animal is quite small. Its body length is no more than 10.5 cm, but this reckless predator enthusiastically devours insects, fishes, amphibians, lizards, mice, and even birds. Their plain tastes in food

make the hunting of frogs and toads quite quickly and successful. The large-breasted tree-frog (*Eleutherodactylus sisypnodenus*) spends most of its time in its burrow. When it hunts in its domain, it can satisfy itself in two hours and then return to its burrow.

Frogs (*Rana*) and tree-frogs (*Hyla*) hunt in ambush. They pick out a convenient position and lie in wait until a suitable victim appears. Toads (*Bufo*) are more active. When it gets dark, they wander along forest and field paths, between the rows in the fields, in gardens with weeded beds, and frequently go where people are, to illumination. The European variable (*Bufo viridis*) and European common (*Bufo bufo*) toads in the southern regions of our country like to hunt at night under burning street lamps. Nocturnal insects, attracted by the light, often strike against the brightly burning lamp and, losing their equilibrium or injuring their wings, drop to the ground. The quick toads snap them up.

When selecting victims, the size of the prey is of major significance. It is quite difficult to determine its size, especially from afar. The European common toad is attracted to objects with angular dimensions from $4 \times 4^\circ$ to $8 \times 8^\circ$, while large objects with angular dimensions of $32 \times 32^\circ$ and more scare them.

Thus, the actual size of the object is not so important as the size of its image on the retina, though there do exist certain limits for the absolute size of the prey. A ball of 13-14 cm diameter scares away common (*Rana temporaria*) and edible (*Rana esculenta*) frogs even if it is far away. Therefore, when the image of the "prey" on the eye's retina becomes too big, hunting stops even before the hunter comes close to it. Prey, to be most attractive by its size, will not violate the permissible angular limits even when it is nearby.

A frog is not interested in any other features of its prey if the size of the mobile object is optimum. If the size of

the “prey” differs from that most favoured by amphibians, then the colour, shape and especially the speed of its motion become important.

As far as small prey are concerned, the majority of anurans are more attracted to round or oval-shaped objects, but toads prefer low, long ones, similar to worms or caterpillars. Artificial baits are not as attractive as live objects. Most likely, the reason is that live objects perform not only translatory movements but also many lesser accompanying motions. They may also produce odours, vibrate, touch the skin of the hunter, and do whatever else that might attract a toad, for example, to a live fly. The position of the victim in space is also significant: a fly, that lands in the vicinity of the frog, seems more attractive than one running around on the ground.

Many problems arise when the hunter sees two mobile objects simultaneously. The bigger one seems more attractive to the toad, but if both objects are of the same size, then the predator attacks the prey which is in front of its snout and nearer to the axial line of its body. The problem becomes more difficult if similar objects are at equal distance from the frog and arranged symmetrically. And in general, if both hunted objects are seen simultaneously by both eyes, then the situation always demands serious consideration. Amphibians sometimes make queer mistakes. When two closely arranged objects move in union, they may be perceived by the animals as one big object, whose “head” and “tail” are seen more clearly. Naturally, the striking shot hits empty space between the moving objects and the hunter remains hungry.

Frogs and toads, waiting in ambush, are very alert. The European common toad (*Bufo bufo*) sees its prey at a distance of 3 m, and the edible frog (*Rana ridibunda*) and the fire-bellied toad (*Bombina variegata*) notice it even 10 m away. They don't trust to chance and never wait till

the victim approaches them, but immediately begin to steal up to it. It is very difficult for the tree-frog to do this because it can rarely move in a straight line. The thick foliage frequently shields its victim but the tree-frog will not be discouraged and never strays from the correct direction.

The hunting habits of the anurans are quite monotonous. When it sees a moving object, the frog turns toward it with a jerk with a high degree of accuracy. The error is never more than $5-10^\circ$, and a maximum turning angle is 180° .

Northern frogs (*Rana septentrionalis*) in the USA when they hunt take up their position on floating plants or at the water edge and sit with raised heads to see better. A dragon fly will be noticed even if it lands 3 m away from the hunter. The frog then dives carefully and approaches the victim underwater. The predator will not attempt to cover the entire distance in one dive because the danger of missing is very great. The frog swims slowly and periodically sticks only its eyes out of the water to check the direction and then again submerges without a splash. The fire-bellied toad (*Bombina variegata*) and the edible frog (*Rana ridibunda*) do the same. They surface under the prey and immediately snap it up. Toads miss frequently, because they overshoot and surface far behind the prey. Fortunately the toad's eyes can look both forward and backward and the hunter, not discouraged, makes an abrupt 180° turn. Amphibians are expert shots. Making a decisive leap toward a rapidly moving object, they aim not at the spot where the "victim" is at the given moment, but, having analysed the victim's direction and speed, predict where it will be at the end of the attack and make an anticipating leap.

The leap of frogs (*Rana*) are instantaneous and accurate. They shut their eyes during the leap and retract them into their sockets in order to avoid accidental in-



Australian tree-frog “aiming” at some prey

juries. The frog extends its legs forward and opens its eyes only at the very last moment. If the direction of the leap is slightly erroneous, the ability of the frog to correct it during flight by turning its head in the required direction and manipulating the webbed widespread digits on its legs is amazing. In spite of the small surface area of the webs, the latter possess a certain lifting force that enables the frog to prolong its flight, or to reduce its speed and so shorten its leap. By moving its legs asymmetrically, the flying acrobat even manages to turn its body a little toward the victim. Moreover, the accuracy of the leap is so great that the hunter often flicks out its tongue while its eyes are still shut. The frog leaps at the victim even if the latter is behind the hunter. These backward leaps result in falling on the back, but in lucky cases the food will have

been seized, which is undoubtedly some consolation.

Tree-frogs (*Hyla*) also manifest very great accuracy in leaping. They have to calculate two interrelated trajectories. One for their head and tongue, which must hit the target, and the other for their legs, which must grasp something in order to prevent falling down. Tree-frogs aim themselves differently from terrestrial frogs. They need only to turn their head in the required direction. They just as easily leap sideways and upward, sideways and downward, and their misses are no more frequent than those of other frogs.

Toads (*Bufo*) are less talented shooters. Approaching the victim to within shooting distance, they aim very carefully before projecting their tongues, sometimes correcting the position of their bodies several times. This is necessary because a lucky hit is possible only if the victim is on the axial line of the hunter's body. Only few species of toads can snap up a prey by turning only the head toward it, or by flicking out the tongue without changing the position of the head.

The sticky tongue allows anurans to hold and pull the victim into the mouth. However, this method is good only for small "game", because the stickiness of the tongue is insufficient to hold large prey. Small prey instantaneously and without visible effort disappears into the toad's mouth. The toad grabs larger victims with its jaws and the front limbs are brought into play to force them into the mouth. It looks quite unattractive: convulsive swallowing movements with long pauses, during which the animal is totally immobile, and only the worm, sticking out of the toad's mouth, wriggles, or the half-swallowed butterfly beats its wing.

Anurans are passionate hunters. They are extremely excited if they miss and frequently fly into a rage. Lightning fast leaps at the victim follow one another and, if it still manages to escape, they croak terribly.

The sandy prairies in the central states of the USA are inhabited by frogs (*Pseudocris streckeri*) that follow a burrowing way of life. Unlike most anurans, which burrow into the soil with their hind limbs, these frogs as well as guinea pig frogs (*Hemisus guineensis*) and Australian burrowing frogs (*Myobatrachus gouldii*), dig into the soil only by means of their forelimbs. The forelimbs of the American frogs are short, massive and without digit discs. If they had nails, they would resemble the limbs of moles, which are excellent tools for digging. You would be mistaken if you thought that they do this simply to spare their hind limbs. They burrow into the earth with the head first only because they feed on insects and worms, living in the soil, and it is more convenient to dig them out with the forelimbs.

Toads and frogs easily endure long famine. During the long cold winter our northerners abstain from food entirely, though, unlike other animals, they lack considerable reserves of fat. The major fat reserve is in the bones and the belly fat body. In winter the amphibians go into a state of anabiosis, reducing energy consumption to the minimum. It is worse for the southerners if a food shortage begins in summer. Desert amphibians feed only in certain short periods, when rains fall and consequently lay down considerable reserves of fat. North American spade-footed toads (*Scaphiopus*) in the deserts of Mexico and Texas burrow into the soil at the beginning of the dry weather and hibernate. Their metabolism is sharply reduced at this time, the consumption of oxygen drops by 80%, and so, the fat reserves are sufficient for the 10 inactive months. But, it may happen that the following spring bring no rain and the period of hibernation will be extended by a year. This is not usually lethal for spade-footed toads. They feed on the proteins of their own body, in the first case on those in the secondary muscles. Females endure long famine more easily than males.

During considerable extension of the hibernation period they "eat" up their progeny, i. e. the eggs formed in the ovary. Toads can survive after such long famines but they will have no offspring that year. Even in warm weather at a body temperature up to 15°C toads can hibernate for more than two years.

The animals come to the surface in spring during the first rainy days. Termites appear at this time during the night after a heavy rain and become available prey for the predators, and during the rest of the year they never leave their underground shelter. The spade-footed toad (*Scaphiopus*) can consume an enormous amount of food at one meal, up to 55 per cent of its body weight. A single dinner supplies the spade-footed toad with sufficient energy resources for more than a year. The multiple spade-footed toad (*Scaphiopus multiplicatus*) needs at least 7 dinners to accumulate sufficient fat and other reserves for the same period, and desert toads (*Chiroleptes platycephalus*) need 11-12 feasts to gain the same results. The point is not in the calorific value of the food but in the efficiency of its utilization by the animal. The burrowing spade-footed toad (*Scaphiopus couchii*) has not been excelled in this respect by any other vertebrate.

The temperature range compatible with the life of anurans is not very great and differs for animals from different climatic belts. During hibernation in the North of Finland, the most favourable temperature for the common frog (*Rana temporaria*) is +4°C, but the animals can endure a short temperature drop below zero. Their motor activity is not reduced at this time. In winter, the frogs burrow into the ooze, rotting algae, holes in the bottom, tangled roots and snags. The use of shelters permits the animals to maintain their body temperature at 0.5° above the temperature of the water.

The northern toad (*Bufo boreas*) preserves its activity even at a subzero temperatures on condition that it

exceeds at least by a little the freezing temperature of the tissue fluids in the toad's body. The Texas toad (*Bufo speciosus*) regains its ability to move only on warming up to +17°C. The northern toad (*Bufo boreas*) is entirely unadapted to hot weather, while the clawed toad (*Xenopus laevis*) can enjoy hour-long sun-baths in water as warm as 32°C. The royal tree-frog (*Hyla regilla*) can survive even if it is heated to 35°C. The woodland toad (*Bufo woodhousii*) is one of the most heat-resistant amphibians. It can survive a brief rise of body temperature to 41°C. Frogs and toads manage to keep within the temperature range predetermined for them by Nature, and are also capable to maintain an optimum temperature at certain times of the day.

It is very important for the younger animals to maintain an optimum temperature. They need to grow, and to do it as fast as possible, because of an abundance of enemies. Early in the morning, when the sun's rays are still weak, young silly toads (*Bufo debilis*) in the South of Arizona and New-Mexico gather in places, where the sun's rays can warm them at an angle of 90°. Thus, the young animals manage to raise their body temperature considerably above the ambient air temperature.

Our northern amphibians are most frequently in need of warmth, but young northern toads manage to find spots warmed up by the sun and maintain their body temperature in the daytime between 20 and 28°C, especially after a copious lunch. The digestive enzymes function more intensively at warm temperatures and the nutritive substances, entering the blood, are immediately used for the construction of body tissues. Any amphibian can raise its body temperature by 5-10°C by utilizing external heat. The Colombian tree-frog (*Hyla labialis*) maintains its body temperature at 11-28°C at an ambient air temperature of 9-21°C even in cloudy weather, utilizing only a small part of the heat rays of the sun. Peru toads live at

an altitude of 4000 metres in the mountains under severe conditions. The air is often cold but the sun's rays enable the animals to maintain their body temperature 3-5°C above the ambient air temperature at fluctuations of the latter from -2 to +15°C.

Amphibians, which live beyond the Arctic circle, are poorly adapted to cold weather. Even a slight frost of 1-2° kills them in an hour. Sometimes frogs are found frozen into the ice. There have been cases when they were revived in warm surroundings. This served a reason to consider amphibians frost-resistant. However, this idea is erroneous. Only those frogs which had frozen into the bottom part of the ice have remained alive. The temperature there is usually close to zero, because the water temperature is never lower.

Amphibians are more afraid of hot weather than of frost. The body temperature can be reduced by evaporation but the effect is very little when the humidity of the air is high. Evaporation reduces the body temperature of a common frog (*Rana temporaria*) only by 0.7-1.1°C under ordinary summer conditions in Europe. The drier the air, the easier is the process of evaporation. At 96-100 per cent R. H. the spade-footed toad (*Bufo fowleri*) can reduce its body temperature only by 0.8°C while at 7 per cent R. H.—by 7.5°C. Evaporation would perform this function excellently in arid regions if the animals did not have to save water. The leopard toad (*Bufo regularis*) gives off 1.1 grammes of water per hour to maintain its body temperature 4.5°C below the ambient temperature. It is very much for a toad because its body weight is only about 20 grammes. The European variable toad (*Bufo viridis*) in the southern Ukraine loses 10 times less water at an ambient temperature of about 20°C. This is why it cannot reduce its body temperature as is done by the leopard toad. The Mauritanian toad (*Bufo mauritanicus*) loses water faster than any other African amphibian and

this enables it to maintain a greater difference between its body temperature and that of the ambient air.

An interesting accessory, preventing overheating, has been found recently in tropical tree-frogs (*Centronella* and *Phyllomedusa*). The skin of these frogs, coloured in different shades of green, possesses a surprising property, which has not been observed in other animals: it reflects the infrared rays of the spectrum almost like the leaves of the plants on which they live. By reflecting the heat rays, they don't warm up and, consequently, do not need to hide in the shade.

The struggle to preserve water is one of the major troubles of anurans. Toads, best adapted to terrestrial life, are covered with skin that is poorly penetrated by water. Besides, toads have more highly developed lungs, which allow them to depend less on dermal respiration than the other anurans. As a result, they can endure considerable moisture losses without any harm to themselves. Our European variable toad (*Bufo viridis*) can lose such an amount of water that equals half of its body weight, and the Californian tree-frog (*Hyla californiae*)—35 per cent, while the common frog (*Rana temporaria*) perishes at a moisture loss of 15 per cent of body weight.

Amphibians hibernate in summer in the arid steppes and deserts. Crawling into deep burrows or fissures in the soil, where some moisture has been preserved, they restore their water reserves by sucking it out of the soil. They never come up to the surface in the daytime. The Australian burrowing frog (*Heleioporus eyrei*) hides at a depth of 30 cm in the burrow that it digs out and closes the entrance with sand. However, it loses about 20 per cent of its moisture during its night hunting even if the air temperature is maximum 25°C. These losses are recovered by the tissue fluids of the consumed victim or by the soil moisture.

The majority of frogs and especially toads can suck

water out of even slightly wet soil. The water is absorbed mainly by a special section of the skin on the belly or the groin, the so-called pelvic spot, rich in blood vessels. The water is sucked in faster here than on the chest or the back. One square centimeter of the skin on the pelvic spot of a horned frog (*Ceratophrys ornata*) absorbs up to 45 mg of water per hour. The leopard frog (*Rana pipiens*) increases its weight by 35 per cent in two days by sucking water from sand of 20 per cent humidity. It needs 4 days to reach the same result at a soil humidity of 10 per cent. The European common toad (*Bufo bufo*) has fine tubular troughs in the skin on the belly that act as capillaries. The capillary action intensify the process of water extraction. The common (*Rana temporaria*), edible (*Rana esculenta*) and terrestrial (*Rana terrestris*) frogs have a similar arrangement. Young burrowing frogs (*Scaphiopus*) have a pelvic spot that occupies only 5 per cent of the skin surface area but it sucks water 18 times faster than the rest of the skin and supplies the organism with 50 per cent of required moisture. This permits the young to hunt during the hottest time of the day. Sitting on slightly moist soil, the young frog manages to suck in through its belly the amount of water that is evaporated from its back. When it becomes an adult, it loses its pelvic spot but gains the ability to accumulate a considerable amount of urea in its blood and tissues. By sharply increasing the osmotic pressure in its tissues, it can absorb residual moisture from the soil, acting like the roots of drought-resistant plants.

Clawed (aquatic) toads (*Xenopus laevis*) manage without the pelvic spot because their habitat is in water.

Amphibians must conserve their available water reserves. The tailed frog (*Ascaphus truei*), inhabiting cold springs in the mountains, lacks reliable protection against evaporation. It loses water so rapidly that it has to stay in water or on a moist substrate even at night. In dry and hot weather the African panther frog (*Rana pipiens*)

clamps its legs tightly to its body, and its belly and chest to the substrate, sharply reducing its skin surface area and, consequently, the rate of evaporation. The leopard frog (*Rana pipiens*) takes up this posture only after losing 15-25 per cent of water.

Tree-frogs (*Hyperolius*) are covered with water-resistant skin and spend several hours in the sun during the hottest time of the day without suffering any harm. It is interesting to note that they wear this water-resistant "coat" only in the dry season. These frogs shed their skin during the first rainfalls and put on ordinary, easily permeable attire.

Another reason for consuming a considerable amount of water is the need to remove waste substances from the organism. The main ones are sodium, potassium and nitrogen, which are excreted with the urine, and, therefore, need water for their removal. Only some representatives of leaf-frogs (*Phyllomedusa*) and flying frogs (*Rhacophorus*), occurring in the highly arid areas of Africa and South America, accumulate uric acid, and all the excess of sodium, potassium and 80 per cent of nitrogen is excreted from the body practically in a dry form as uric acid salts. This makes it possible for them to maintain their activity during the dry season, managing to exist on the water contained in the insects they feed on.

It is impossible to count on restoring water reserves in the Australian savanna, where in summer the soil dries to a great depth. Even insects disappear there at this time of the year. Local toads save themselves by making extremely large reserves of water. With this reserve, the toad hides in a deep burrow in the clay soil. A water-tight cocoon soon forms from the solidified mucus and scale-like cells in the skin, in which the animal waits patiently for the next rainy season. Once, Australian aborigines, roaming across arid plains, used toads as the only source of water.



The lymphatic sacs of Australian *Litoria* are easily seen

It was supposed earlier that the water was stored in the lymphatic sacs, that represented empty space under the skin. It is hardly true. The matter is that they are best developed in aquatic amphibians, in clawed toads (*Xenopus laevis*) and frogs (*Rana papui*). Most likely the lymphatic sacs perform an opposite function: assist in disposing of the water that continuously penetrates through the skin. It is quite an important and complicated problem. It is dangerous for young edible frogs (*Rana esculenta* and *Rana ridibunda*) and the Far East frogs (*Rana semilpicata*), as well as for the European common (*Bufo bufo*) and the European variable (*Bufo viridis*) toads to stay in the water. They perish as a result of an excessive accumulation of water in only 5-12 hours.

Young frogs can stay in the water for 1-2 days at the age of 3-4 weeks. The water is no longer dangerous to them when the frogs grow older. The skin of aquatic frogs is poorly penetrated by water and the animal treats it with the secretion of its skin glands. The mucus of the disk-tongued frogs (*Discoglossus*) flows over the skin surface and forms a thin film, which prevents the penetration of water into the organism.

Frogs and toads lead a settled mode of life and occur on a small territory, to which they are strongly attached. The woodland toads (*Bufo woodhousei*) in the USA inhabit the same areas in the forests from year to year and never wander away more than 20-30 metres from them. The territory of the tropical male cloudforest frog (*Atelopus oxyrhynchus*) amounts to 50-60 square metres, and that of the female—about 30 square metres. Still bigger (up to 130 square metres) is the territory of the large-chested webless frog of the genus *Eleutherodactylus*. One collared tree-frog (*Colostethus collaris*) manages with a tiny plot of 0.01 square metre. The hosts are extremely jealous of the inviolability of their borders. When their territory is invaded, they demonstrate their bright-yellow pulsating throats to the enemy, push the unwanted guest with their heads, and, if all this is not enough, leap on its back. Fights are more often between females. Males are usually more tolerant.

Edible frogs (*Rana esculenta* and *Rana ridibunda*) lead a settled way of life but it is unclear whether they own strictly bordered plots. Nevertheless, a certain distance between the neighbours is always preserved on the bank of the pond, at least 30-50 cm on land and 20-30 cm in the water. Violation of this distance leads to fights no matter who was the trespasser, male or female.

Violent fights break out between young tree-climbing frogs (*Phyllobates*) in Venezuela. The fighters grasp each other with their forelimbs and, standing upright on their

hind limbs, try to throw one another on their backs.

The Trinidad tree-frogs (*Colostethus trinitatus*) live under a matriarchy. Only the females are owners of plots, while the males never stay long in one place. The female defends her tiny plot, which is from 0.3 to 1.0 square metre, even from a visiting male. This mutual hostility and division of territory prevent high population density and ensure the frogs and toads, and their tailed relatives, success in hunting and sustaining life.

It is impossible to count the number of enemies of anurans. Mammals, birds and reptiles are ready to dine on frogs. They are consumed by big and strong predators as well as by such small creatures as common and water shrews. Very small animals are found among the enemies of frogs. In Australia small frogs are attacked by spiders, mantises and large carabids. Large ants exterminate very young frogs, up to 11-12 mm in size.

The majority of frogs and toads are entirely defenceless creatures. When they meet any animals bigger than they are, they flatten against the ground and bend their head down in a peculiar way. Frogs run away from the bigger animals that move actively in their direction. As was mentioned earlier, only very poisonous creatures lack this reflex.

Some frogs defend themselves actively from small predators. Our common spadefooted toad (*Pelobates fuscus*) inflates itself, rises on unnaturally straightened legs, opens its mouth and emits loud sounds. The predator gets scared and retreats. Even a human, who accidentally sees this performance, will think twice before touching the frog. The coloured frog (*Kaloula pulchra*), guinea pig frog (*Hemissus guineensis*), narrow-mouthed (*Breviceps*), European common (*Bufo bufo*), running (*Bufo calamita*), marine (*Bufo marinus*), and some other large toads inflate themselves and take an aggressive pose in case of danger.

Sometimes the bellicose amphibian leaps at its enemy and butts it with its head.

Large tropical frogs and toads bite quite actively. Their teeth may injure a predator. The Burmese toad (*Megophrys carinensis*) attacks its enemy bravely. The attack may be repeated 2 or 3 times, during which the toad or frog gets very excited, but if the attack makes no impression, it is always ready to run away.

Our toads (*Bombina*) demonstrate their red or yellow belly to the enemy at time of danger. In spite of the difficulty of doing so, they manage to tear their front feet off the ground, clasp them to their bodies, and bend the head and sacrum upward. As a result the toad looks like a toy rocking-chair and the bright belly is clearly visible. If the enemy is not frightened away, the toad burrows into the soft soil as fast as possible. The spade-footed toad (*Pelobates fuscus*) behaves in a similar manner. It burrows into the soil almost vertically by moving its hind limbs rapidly up and down. It needs only a few minutes to disappear completely if the soil is soft.

Some bright-bellied frogs turn over on their backs at an attempt to confuse its enemy by an instantaneous change of the scenery. There are many ways of escaping. They can climb up a tree, hide in a bush by going up a thin branch, or, finally, leap into the water. Even the red-footed frog (*Rana aurora*), which usually avoids damp places, takes to water in case of danger. If a toad is unable to escape, it starts a fight with the enemy, using its forelimbs to push away the head of a grass snake or that of a serpent. Gladiator frogs (*Hyla boans*) are quite aggressive. Their bellicose character is quite justified because they are armed with a well developed sharp spine, which can inflict painful wounds.

The main identification of an enemy is its size. Anything that exceeds its own size calls forth a defence reaction in the frog, because everything that is unappetizing is

terrifying. There is no clear distinction between the sizes of a prey and a predator. Hence, other properties are important: the colour, the sounds emitted by the object, vibration of the substrate or the surrounding plants, the speed and direction of its locomotion.

The retreat of anurans is usually purposeful. Frogs always run toward the nearest shelter, to thick grass or toward bushes. If the enemy is between the frog and the shelter, the frog has to break through. The animals usually prefer to slip by the enemy and hide rather than to run across open land. Amphibians, inhabiting water bodies, dive into the water. They are extremely careful and an enemy rarely manages to cut off the retreat to their native habitat. Nevertheless, if it happens, nothing will make the frog run in a direction away from the water.

In case of danger tree-frog (*Hyla*) hide and, using their camouflage, stay immobile until the very last moment and then leap to an earlier picked branch.

When running away from an enemy, anurans calculate the degree of danger very precisely and behave accordingly. If the danger is not very great, aquatic frogs, sitting on the bank, leap into the water and swim a little away, sticking out their snouts carefully. But if the danger is great, they dive to the bottom, burrow into the silt, or hide in the thicket of aquatic vegetation.

Frogs and toads will not leave their shelter for 10-20 minutes after being frightened. When they finally surface and get out on the grass, they behave very carefully, ready at any moment to run away at the slightest suspicious movement.

Frogs orient themselves very well in their little world and know how to find their territory. The European common toad (*Bufo bufo*) walks all its life along a closed circle. When it wakes up in spring in its winter shelter, it goes to the breeding grounds. The path may sometimes be quite a long one, from 6 to 12 kilometres. Having

finished its spring chores, the toad takes off for its summer residence, and when the weather turns cold, returns to its winter quarters. Edible frogs (*Rana ridibunda*) are just as persistent in their habits and, unless especially necessary, never change their winter quarters or individual plots.

It is known that anurans, which have been moved one kilometre from their homes, find their way home across entirely strange territory. At an air humidity of 75 per cent our toads (*Bombina*) always return home to their native aquatic habitat. Orientation is disturbed at an air humidity of 100 per cent, but, apparently, the animals feel themselves at home everywhere in wet weather and feel no need in returning to their homes.

Bull frogs (*Rana catesbeiana*), leopard frogs (*Rana pipiens*) and tree-frogs (*Hyla*) find their way home quite easily. How they manage to do it is still a mystery. With the majority of frogs neither vision, hearing nor scent participate greatly in the process of orientation. But terrestrial frogs (*Rana terrestris*) are entirely disoriented if scent is eliminated.

Some amphibians can use the sun, moon and stars for orientation. Even the young Mexican toad (*Bufo valleriensis*) can do this. The accuracy of orientation is easily disturbed if the young are kept for a long time in darkness. These toads don't use scent for orientation. But males search for a spawning water during the breeding season only by the smell of the water. Females don't use the sense of smell very much. They arrive at the spawning grounds after the males, finding it by the songs of their future mates.

Navigational habits are inherited, but the reference points have to be specially memorized. Noisy frogs, living on one side of a pond, put into a special enclosure, where they are deprived of all reference points beside the sky, move in the direction corresponding to the direction from

the water to the bank. They need only three hours on the opposite bank of the pond to memorize the navigational reference points of their new habitat. Now they will move in the enclosure just in the opposite direction, corresponding to the direction from the water to the bank with their new shelter.

Compass orientation has been discovered in the bull frog (*Rana catesbeina*), the Mexican shore (*Bufo valliceps*) and some other toads, in spadefooted toads (*Bufo fowleri*) and leaf-frogs (*Phyllomedusa*). If they are kept for a long time in darkness, they become disorientated because their correct time count is disturbed.

Specialists, studying the psychics of animals, have always considered frogs and toads to be animals that are poorly capable of learning anything.

And indeed, the strict innate regulation of many behavioural actions eliminates their major transformation as a result of training. And this led the researchers into error, when training was performed without consideration of inherited behavioural programs. Frogs and toads under ordinary conditions are not scared even by loud sounds. Amphibians are interested in sounds only in spring, and even at this time they listen only to the voices of their relatives and demonstrate complicated behavioural reactions only in response to their audible signalling. It is not clear why Nature has not provided for the possibility of defence reactions in response to sound stimuli. This design imperfection of the brain is the reason why it is impossible to train anurans to be afraid of sounds, or, as the specialists would say, to develop a conditioned defence reflex.

Food gathering behaviour is still more complicated. It is manifested only at the sight of mobile objects and it is impossible to train frogs to run like mad to the feed box at a flash of light and, the more so, on hearing a signal, as can be done very well with the silliest dog. This is also

associated with the design specifics of the amphibian's brain. However, the latter is no indication of the brain's imperfection. It is quite easy to train hungry frogs and toads to gather at the feed box. They can even learn that it is worth while doing so only when a light is burning above the box.

Nevertheless, frogs are not quite indifferent to sounds. Though it has proved impossible to train them to do something by an audible signal, it has been found possible to train them not to do something. Several more capable European common toads (*Bufo bufo*) have learned in the laboratory that it is not worth while grabbing a dead fly if its demonstration is accompanied by a certain sound. It was really not worth while swallowing the fly because the experimenters had soaked it in citric acid, and it had become so unpalatable that many animals abstained from flies to be on the safe side.

It is not easy to teach old-time hunters to be indifferent to prey. A fly, that has landed on the glass wall outside the terrarium, will be attacked immediately. The leaps will follow one another despite their complete futility. It is almost impossible to train anurans to ignore mobile objects outside their transparent shelter. But the situation changes if live flies are covered with a glass and placed inside the terrarium. After a long series of attacks the animals will turn their backs to the glass so as not to see the flies running to and fro.

Amphibians can be trained not to touch artificial baits, imitating worms, beetles or butterflies, not to snap baits painted red, baits of certain size or even shape, though the latter is very difficult for frogs. It is interesting that, having sealed the left eye of a toad and trained it not to attack a red model of a worm, which it can see only with its right eye, the process of training will have to be repeated in order to teach it to recognize the model with the left eye.

This reflects the specific manner of acquisition, processing and storage of information on the environment in the brain of anurans.

Frogs and toads can be trained to find their way in a labyrinth, to get out of it to an arena, or to enter a shelter, where it is sufficiently humid, not very hot and semi-dark. It is enough for the European variable toad (*Bufo viridis*) in a suitable shelter to be once or twice to remember the way to it.

Genetic instructions are far from perfect. They must be supplemented with individual experience. Only young and inexperienced frogs and toads grab feed indiscriminately. Frogs will not touch bright poisonous moths at breeding grounds. This is not surprising because one contact with a poisonous caterpillar will make the frog remember the unpleasant consequences of this acquaintance. European variable toads (*Bufo viridis*) easily remember poisonous spiders and distinguish them easily from other "game". Wasps, bees and bumble-bees with a strong sting and poison glands, do not arise any suspicion in toads before the first contact. But after one or two bites the animals avoid any future contacts. Thus, anurans always learn something new. And it must be admitted that they are quite assiduous in their studies.

Anurans, even the most poisonous ones, rarely live up to very old age. Nevertheless, if they manage to survive all the dangers that await them in their childhood, they live to quite a reasonable age. The maximum lifetime of the European common toad (*Bufo bufo*) is 36 years, the clawed frog (*Xenopus laevis*) lives for 33 years, toads (*Bombina*) and the paradoxical frog (*Pseudis paradoxa*)—29, the tree-frog (*Hyla arborea*)—22, the common (*Rana temporaria*) and edible (*Rana ridibunda*) frogs—18, the bull frog (*Rana catesbeiana*)—16, and the toads (*Pelobates*) and edible frogs (*Rana esculenta*)—10 years. The

long lifetime is another reason for continuous learning. Only short-lived animals can remain ignorant.

Information Service

The life of any organism is closely associated with the environment, as it receives from it food, water, oxygen. Any living creature has to come into contact with its like in order to have offspring and to ensure further procreation of the species. It is pertinent to be well informed in order to survive. Amphibians receive a considerable part of their information by vision. The air medium is favourable for this. It is more transparent and lighter than water. Hence, amphibians are more farsighted than fish. To prevent drying, the amphibian's eyes are covered with mobile eyelids, and there are three to each eye: the upper, the lower and the third eyelid, which is a nictating membrane in the front corner of the eye. The eyelids are scarcely mobile and to close its eyes, the amphibian has to retract them into the eye sockets, as when swallowing food. The second distinction from fish is the availability of lacrimal glands to wet the eye cornea.

Terrestrial frogs and toads have big eyes, but aquatic frogs have tiny eyes, while in the majority of adult cave amphibians the eyes are reduced and grown over with skin. The olm (*Proteus anguinus*) is unable to demonstrate even traces of eyes, as they have entirely disappeared.

The eyes of the amphibians have a light-sensitive part, the retina, and an optical part, the cornea and lens for focusing the image on the perceiving elements of the cornea. Light rays are refracted in the air mainly by the cornea of the eye, and by the lens in water. To look at objects located just under their noses, the frogs have to adjust the optical systems of their eyes. Without such additional

adjustment the zone of clear vision is at a distance of 13-33 cm.

The process of focusing is the same as in fish. Instead of changing the curvature of the lens, as do all the higher animals without exception, amphibians move the lens along the optical axis of the eye, bringing it closer or moving it away from the retina. Active focusing is performed in fish by moving the lens backwards, while amphibians adjust it forwards.

The pupil of frogs looks like a horizontal slit. It is very convenient for animals that are on the watch for prey on the water surface. Toads, who hunt their prey actively more often than anurans, need wide vision to both sides and upwards. Hence, their pupil may be rhombic or approach a vertical shape, for example, in tree-frogs (*Hyla*) it is triangular or rectangular, while in urodeles it is oval.

The eyes of the majority of anurans stand out clearly above the skull and have a wide field of vision. Terrestrial frogs see equally well forwards, sideways, upwards and backwards, and a considerable part of their surroundings is seen simultaneously by both eyes. The vision of urodeles is more limited. The zone of binocular vision of newts is only in front of the animal. It is quite narrow, no more than 40°. The animal is unable to see anything directly above its head or behind it.

The light-perceiving elements, which are red and green rods, simple and twin cones, are in the retina. The resolving power of the eye depends partly on the total number, but mainly on the density of the photoreceptors in the retina. Therefore, with a similar number of rods and cones a small eye will have a more acute vision than a big eye. The little eyes of the bistripped salamander (*Eurycea bislineata*) are considerably more acute than the big eyes of salamanders (*Ambystomatidae*).

The photoreceptors are not distributed uniformly. The

Mexican salamander (*Ambystoma*) and terrestrial frogs and toads have a horizontal line near the retina equator with an increased density of rods. An instantaneous reaction is stimulated in the animal when this line is crossed by the image of a prey or a predator. Tree-frogs (*Hyla*) have no such line in the retina because these creatures are not interested greatly in the sky-line. The density of the receptors is 2-3 times greater in the central part of the retina than at the periphery.

Terrestrial and marine animals use rhodopsin as the light-sensitive element in the photoreceptors, and those inhabiting fresh water—porphyropsin. The short-wave rays of the sunlight hardly penetrate yellowish water where there is a mass of microscopic algae, while porphyropsin is more sensitive to long-wave light. The animals, who spend a part of the year in water and another part on land, have to readjust their photoreceptors each time. Most of the rhodopsin is replaced by porphyropsin in newts and salamanders who return to their water habitat in spring for spawning, while in summer, when they change their water residence for terrestrial conditions, porphyropsin is again substituted by rhodopsin. The larvae and tadpoles also use porphyropsin, which is then replaced by rhodopsin. Both these pigments are contained mainly in the red rods, while the cones utilize another light-sensitive substance, namely, iodopsin.

It was a great surprise for the scientists to learn that the frog's eye sends processed information to the brain, informing it of some properties and features of the objects perceived. But, the latter fact is not strange. In essence, the retina is a part of the brain that separated from it at the earlier stages of ontogenesis and moved to the periphery. Beside the layer of photosensitive cells, rods and cones, it contains, as should be in the case of cerebral tissue, layers comprising nerve fibers and nerve cells. As a result of the different types of links between the receptors

of the retina with the ganglionic (nerve) cells located in the retina, the receptors are capable of distinguishing certain properties in the viewed objects. For this reason they have been called detectors.

Five types of detectors have been found in the frog. The most important one is the dark spot detector. It sends information to the brain when a small dark spot moves within the frog's visual field. The detector, which has been called the insect-revealing detector, will not react to a light spot. No reaction will occur even when the frog is given a real live fly, illuminated so that it seems much brighter than the background. The signals of the straight-edge detector assist in going round obstacles. The detectors of moving contrast, which cause a defence reaction, signal on any rapid motion in the visual field of the animals.

The darkening detectors send signals on changes in the light intensity. They are used when seeking shelter. And, finally, the darkness detectors react only to a slow change in the general illumination. The signals of the detectors are sent apparently without further processing by the brain directly to the executive organs, ensuring maximum speed of reactions.

Certain specialization may be observed in some amphibians in the detectors reacting to the motion of an object. They react only to motion in certain direction: to an approach or removal of the object, to its movement from the left to the right, or vice versa. Detectors of motion direction have been found in the spotted newt (*Triturus vulgaris*), the mud puppy (*Necturus maculosus*), the common frog (*Rana temporaria*) and the bull frog (*Rana catesbeiana*).

Urodeles possess the most primitive detectors. Not a single one of the three types they have coincides fully in its properties with the insect-revealing detector, which is so important in frogs (*Rana*). Only four types of detectors

have been found in toads (*Bufo*). The characteristic peculiarity of the detectors in salamanders (*Salamandridae*) is their sensitivity to the slightest movements and their ability to see tiny objects. The detectors of the salamanders react very well at light intensity ten times less than that required by frogs and toads.

The detectors are not perfect. They work well while the frog deals with one fly. But the greater the number of prey, the weaker the reaction of the detectors. This effect is explained by lateral inhibition, the essence of which is that a detector, revealing a dark spot, inhibits the reaction of the neighbouring detectors, including those that have also detected a dark spot, being itself inhibited by the effect of the latter detectors. Hence, when several insects appear in the visual field of the frog simultaneously, it does not see them and no reaction occurs. This defect of vision is not found in newts. The latter are not embarrassed by any number of moving objects on condition that they do not coalesce into one stirring cluster, and maintain a certain spacing between each other.

The vision of amphibians, as in other vertebrates, is characterized by an interesting peculiarity: they are blind to immobile objects. This defect is compensated in mammals by the permanent mobility of the eyes, which continuously perform slight oscillating movements, thereby making the objects visible. The eyes of frogs and toads are immobile. It is true that breathing causes some displacement of the head, but it is too little and does not assist vision. Nevertheless, the immobility of the eyes is a blessing for the amphibians. The surrounding world is too complicated for the primitive brain of the frog. If it saw several objects simultaneously, it would be unable to deal with such a chaos of visual impressions. But as it is, not a single moving object, no matter where it comes from, remains unobserved, because it is the only thing seen by the frog. Other visual impressions do not distract

it. Amphibians are unable to see multiple stereotype repeating movements. Quivering leaves, pendulum swinging branches, ripples on the water surface from the continuous small waves do not distract the amphibians from being constantly on the alert. They are simply blind to these movements.

Although blind to immobile objects during locomotion, the amphibians demonstrate excellent skill in orienting themselves in the environment. If a European variable toad (*Bufo viridis*) sees an earthworm behind a small fence, it either goes round the fence, or squeezes through a slot between the boards, deciding from afar which way is shorter: going round or squeezing through the slot. An adult toad can squeeze through a hole more than 3 cm in diameter. It makes an accurate estimate from a distance of 5-15 cm and loses this ability only when it is more than 20 cm away.

If a calmly resting frog is frightened suddenly, it does not hit its head on a stone or the trunk of a nearby tree. Frogs always manage to escape from an open pail, box or bath, leaping over the edge at the first attempt and never touching the edge. They leap just as skillfully through a small round hole in the pail's lid, the diameter of the hole being only 6-7 cm. They do so even if the hole is not at the edge but in the centre of the lid.

It is interesting to note that all the sensory organs function more acutely during the nuptial period. If an object, which is not very big, is placed on the spawning ground of European common toads (*Bufo bufo*) at a small distance from the assembling males, it will not be missed even if it is not emitting any sounds, vibrating, or having a scent like a female, and remains immobile. After some time, the most active male will leave the groupage of males and will approach the object that invaded the spawning ground. The male will press its neck to the object and grasp it with its front limbs, as if it were a female.

This testifies to the fact that the animals are sometimes capable of noticing immobile objects.

Higher animals, by estimating automatically the degree of their eyes' convergence, accurately calculate the distance to the objects they see, but more often they use auxiliary means to this end. Knowledge of the real size of many objects simplifies estimation of the distance and assists in determining the size of the unknown objects nearby. Amphibians use the same criteria. When common frogs (*Rana temporaria*) were placed in special empty chambers with diffuse light, where the animals had nothing to hold their attention, they lost the ability to determine the size of distant objects. Even the appearance of tremendous (from the frog's point of view) balls, 10-20 cm in diameter, caused a reaction similar to that engendered by a food object. And though the frogs made no attempt to approach the balls, they never took to their heels, as they would have done under any other conditions.

Frogs and salamanders are extremely bad at distinguishing the shape of objects, especially those of small and immobile ones. Toads are unable to find the exit from a room by using for orientation squares, triangles and circles above the holes. All amphibians with eyes can apparently discriminate between small rectangles and squares, as long as the figures are moving. Unique visual faculties have been found in fire salamanders (*Salamanca salamandra*). The animals needed only five days to memorize the pattern of the floor in front of the entrance to their shelter. The pattern was made up of black and white stripes of a certain configuration. When let out on an arena, the salamanders picked out parts of the floor with the known pattern.

It was impossible for a long time to determine whether amphibians were capable of discriminating colours. The electric reactions of the retina indicate that newts and

salamanders have two types of colour-sensitive receptors for blue and yellow shades, while frogs and toads have three: for blue, green and yellow colours. The majority of amphibians see evidently the surrounding world in a combination of these colours. It is possible to train crested newts (*Triturus cristatus*) to find food, orienting by the colour of the feeding-troughs, while the larvae of the fire salamander (*Salamandra salamandra*) "hunt" small round discs of an orange, yellow, yellowish-green or blue colour. A piece of food, attached to the back side of the disk, was a reward for a correct choice. Young amphibians discriminated edible "game" from empty discs, that were coloured in the adjacent shades of the colour scale, including 24 tints. The European common toad (*Bufo bufo*) possesses good vision. They never confuse blue and gray colours of similar brightness.

The capability of the frogs to discriminate between poorly illuminated colours is very important. A Russian proverb says that all cats are gray at night. And we really do lose colour vision in the twilight, but a tree-frog (*Hyla arborea*), even at an illumination intensity of 0.07 lux, preserves the sense of colour. However, all the colours disappear at this illumination for the European common (*Bufo bufo*) and red-bellied (*Bufo calamito*) toads, as well as for the midwife toad (*Alytes obstetricans*) and they no longer distinguish them.

The ability of the amphibians to change the colour of their skin is associated with their vision. It has been mentioned earlier that the colour of the skin depends on the air temperature, humidity and the emotional state of the animals, but light is the main cause for a change in the colour. The animals react not to the general illumination, but compare the amount of light, coming from above, with that reflected by the background on which they are located. This ratio will be high for an animal on a black background and, therefore, its skin will darken. The

lighter the background, the lower the ratio, and the animal's skin begins to turn lighter. A white background reflects up to 80-95 per cent of light, while a black background reflects a maximum of 5-10 per cent.

The light from the background affects mainly the bottom part of the retina, while information on general illumination intensity is sent to its upper compartments. The brain compares the recorded information and decides whether the animal's colouration corresponds to the background and how it ought to be changed. Frogs can easily be confused. When the bottom part of its pupil is painted with opaque ink, the animal believes that it is on a black background and its skin begins to darken.

A comparison of the illumination intensity alone is certainly not sufficient for animals who can not only get darker or lighter, but can also change their colour. These amphibians ought to be able to determine quite accurately the wavelength of the light reflected by the background. However, scientists know too little about this.

Few people know that frogs are three-eyed creatures. Beside the common pair of eyes, amphibians have a vertex organ, or epiphysis, which is sometimes called a third or a forehead eye. It is possible to discern a forehead spot on the head of some frogs in the gap between the upper lids, rather like a small wart, which is slightly visible through the skin. This is the epiphysis. It appears in the tadpole as a tiny bubble, an outgrowth of the dien-cephalon. During its development, the bubble splits into two parts: the upper one (the forehead eye) leaves the skull cavity, retaining communication with the brain by means of a nerve bundle, comprising 20-85 fibers, while the bottom one turns into a pineal organ (or pineal gland). It remains in the skull cavity and communicates with the brain via a thicker bundle, containing up to 250 nerve fibers.

The forehead eye had a common visual function in

ancient amphibians and reptiles that are long extinct. This is confirmed by the big hole in the upper part of the skulls of giant pangolins. It is nothing but the third eye socket, whose size is but little inferior to the lateral ones.

The structure of the forehead eye confirms its visual function. It is possible to find in it a lens, a vitreous body, something like a retina with light-sensitive cells, the rudiment of a tunic and an ophthalmic nerve. Beside that, the third eye also contains glandular cells, which degenerated in higher animals into an important gland.

The receptor cells are in the pineal organ and in the forehead eye cavity. They resemble common rods and cones, react to light, including the ultraviolet part of the spectrum, and are sensitive to colours. They function but are unable to apply their faculties fully beneath the skin or in the cavity of the skull. About 0.3 per cent of light penetrates into the cavity of the frog's skull. The sensitivity of the photoreceptors makes the latter react to diffuse sunlight, and the forehead eye sees even in twilight.

What is the purpose of this strange formation? The functions of the third eye have still been studied very little. However, it has been possible to establish that it is used by cold-blooded animals as a thermometer. Considerable deviations of the body temperature from the optimum level are liable to have serious consequences. In such cases the forehead eye sends a warning signal.

The third eye is more efficient in some respects than the ordinary ones. It is known that it assists the frog in perceiving linear polarization of light and compass orientation. In the blind larvae of clawed frogs (*Xenopus laevis*) it sends a signal to escape, if a shadow falls on the babies. And finally, the forehead eye participates in synchronizing the physiological processes of the amphibian's organism with the rhythms of the environmental illumination, in changing the camouflage colouring of the skin. Even the amphibian's larvae darken and become

lighter by this means, but they do it in a different way than adults. Tadpoles get lighter in darkness and darken in light. This reaction is performed without the participation of the lateral eyes and, if the latter are removed, the sensitivity to light does not change.

The capability to change their camouflage is preserved in amphibians that are deprived of all three eyes because the chromatophores themselves possess light sensitivity and react to illumination by distributing the pigment to its outgrowths. However, the brain, receiving information from the eyes, usually suppresses this activity of the dermal pigment cells.

The sensitivity of the melanophores in leaf-frogs (*Phyllomedusa*) is so great that local changes occur easily in the camouflage colour of the skin. The frogs can change the colouration of their body and even recover the pattern of the background on their skin owing to the functioning of the eyes and the sensitive pigment cells.

The vestibular analyzer, the organ of equilibrium, is the next acquisition in the evolution of the animal world. These paired formations inform on the changes in the position of the body and on its acceleration.

The development of audition has been associated with the necessity of analyzing sounds produced by the animals themselves. They have not been interested in other sounds.

The acoustic analyzer is an organ capable of detecting rapid but insignificant fluctuations of pressure in the environment. Two tiny papillae, comprising very few receptor hair cells, are contained in the internal ear. One papilla is more sensitive to high-pitched sounds. It is used mainly in air, while aquatic animals, olms (*Proteus anguinus*) and salamanders (*Amphiuma means*), lack it. The other one serves for perceiving low-pitched sounds and vibrations and so is lacking in many terrestrial urodeles. The middle ear is designed as a bridge for the

acoustic waves from the exterior to the internal ear. In most anurans the middle ear is separated from the exterior by a tympanic membrane. Its vibrations are transmitted by a system of tiny bones to the oval window and fluid, surrounding the papillae, thereby stimulating the receptor cells. The area of the tympanic membrane is considerably greater than that of the bone pressing on the oval window, and this ensures at least a 10-fold gain in mechanical work. The sensitivity of the acoustic analyzer is amazing. To stimulate the receptor cells, it will be enough to displace the tympanic membrane only by 0.000 000 000 6 mm, which is 1.5 times less than the diameter of a hydrogen atom.

The tympanic membrane of the terrestrial animals performs an extremely important function: it transforms the vibrations of the air into vibration of the fluid in the internal ear. Sound cannot penetrate directly through the skin, muscles and bones of the skull without participation of the tympanic membrane because the acoustic waves attenuate practically by 99.9 per cent at the interface of the two media (air-skin). However, the acoustic properties of the body tissues are quite close to the acoustic properties of water and the losses are very small at the boundary between the water and the skin. The tympanic membrane is usually lacking in those urodeles that are closely associated with water. Caecilians (*Caeciliidae*) lack it. Sounds lose their significance for animals permanently inhabiting the underground world. The information of vibratory oscillations is more important in this environment. Toads (*Bufo* and *Pelobatus*) lack a tympanic membrane owing to their habit of spending their time in water or in burrows.

It would appear that aquatic animals would find a special acoustic canal unnecessary. However, the papillae function effectively only when the acoustic waves penetrate the internal ear only in certain spots. The bones of

the mandible, closely adjacent to the acoustic bones, make up the acoustic canal in aquatic amphibians. This canal is used most efficiently when the animal is lying with its head pressed to the ground. It is highly important for the amphibian's larvae, and for land salamanders and caecilians, when transmitting the vibration of the soil to the internal ear.

The bones of the forelimbs evidently serve as the secondary acoustic canal. Acoustic vibrations of the soil, reaching the shoulder blades, may reach the auditory ossicles and the internal ear through a special muscle. This path is less effective, because considerable losses of acoustic energy occur in the joints and at the transition from the bone to the muscle.

The most efficient route of acoustic transmission is the circulatory system. It has developed two relatively independent sound paths. Acoustic waves, penetrating through the skin on the head and throat, inevitably run across a branching network of subcutaneous venous vessels. Liquid, including blood, is an ideal medium for sound propagation. Running along the sufficiently large lateral vein in the head, the acoustic waves reach the internal ear, because the vein approaches closely the ear's entrance and passes round the auditory ossicles or their rudiments.

The acoustic waves can easily penetrate the skull via the circulatory system and reach the auditory papilla by the middle cerebral vein. The latter papilla perceives low-pitched sounds. These two paths are most effective for the perception of sounds in water. Toads (*Bombina* and *Pelobates*), which lack a tympanic membrane, apparently use them also in air.

Each species of animals reacts to sounds only within a limited range of frequencies. A human begins to hear a sound as a continuous one only at a frequency of 16-18 oscillations per second. When the frequency exceeds

20 000 per second, the human ear cannot perceive such rapid pressure changes and it seems that complete silence has fallen all around.

Data on the auditory threshold is currently available only for a few species of amphibians. The leopard (*Rana pipiens*) and green (*Rana clamitans*) frogs hear approximately the same range as humans. The sounds they perceive are within the range of 30-15 000 Hz. Toads (*Bombina* and *Pelobates*) perceive sounds in the range of 200-3500 Hz. The ambient temperature is of vast significance as it affects the speed of the nervous impulses in the fibers of the auditory nerve. The conductivity is reduced at low temperatures and the frog no longer perceives high-pitched sounds. Edible frogs (*Rana esculenta*) stop perceiving sounds in air even at 8°C, if their frequency exceeds 100 Hz. The fire-bellied toad (*Bombina variegata*) is deaf to sounds above 500 Hz at 5°C, while the midwife toad (*Alytes obstetricans*) hears them normally, but at 20°C its hearing intensifies greatly. The common frog (*Rana temporaria*) hears best at 15°C, while the red-bellied toad (*Bombina bombina*) finds it better at 16-22°C.

It is important for the animals to know where the sound comes from. The green tree-frog (*Hyla cinerea*), on hearing the call of a male, turns toward the sound, but before going to it for a rendezvous, turns its head several times from side to side to check the direction of the call. Her direction is always correct if the distance to the male is no more than 4 metres. It should be remembered that amphibians use acoustic information only in their amorous encounters. Defence or nutritive reactions are never stimulated by audio signals. Only the voices of their own kind are of real significance for the amphibians. Marine toads (*Bufo marinus*) feed systematically on crickets, very noisy creatures, who adore to make music continuously and in self-oblivion. However, even the most experienced hunters will not approach the cricket

until they see it. Toads never attempt to find "game" by the sounds the latter emit.

Amphibians have been the first terrestrial animals to develop a vocal apparatus, the prototype of the vocal organs in higher vertebrates. Its main part, the vocal ligaments, may tense and then the air flow causes them to vibrate, thereby producing a sound. The vocal talent of anurans has gained wide renown, but very few people have heard the voices of newts and salamanders. They produce very weak sounds, which are imperceptible to the human ear at a distance of 1-2 metres. The crested newt (*Triturus cristatus*), the European cave (*Hydromantes gormanii*) and fire (*Salamandra salamandra*) salamanders, the spotted salamander (*Ambystoma maculatum*), the salamander (*Amphiuma means*) and other salamanders can creak, squeak, and produce a low whistle, repeating these sounds systematically with brief intervals.

Frogs and toads have sound generators and amplifiers. The resonating sacs, that are frequently very big and swell up on the throat of many male anurans, amplify the sound to a considerable extent. Owing to the resonating sacs these little creatures (one ought not to forget that even the biggest amphibian is rather small in size) can produce sounds of amazing intensity. When America was being colonized, the concerts performed by choruses of spadefooted toads (*Bufo fowleri*) were audible for many miles, and frequently frightened the white immigrants, because the stentorian, sinister voice of these animals resembled the war cries of Indians.

Tree-frogs (*Kaloula pulchra*) cry out very loudly because they inflate both the resonating sac and their entire bodies. These frogs easily suppress human voices. The bull frog (*Rana catesbeiana*) has a strong voice, and people hearing it for the first time, will usually not believe that it is generated by a frog and not by a big animal.

Dickerson, an American zoologist, transcribes it as follows: mmm-jag-oow-rram. In order to ensure a complete imitation, these sounds must be generated altogether, in a loud voice and into a hole in an empty barrel. The North-American tree-frog (*Hyla regilla*) can produce loud creaking sounds. It is not surprising because the resonating sacs are three times bigger than its head. The sound, emitted by the cricket-frog (*Acris*), can be imitated by hitting two round stones against one another. The cry of the tiger frog (*Rana tigrina*) resembles the noise produced by tearing fabric. The voice of the narrow-mouthed tree-frog (*Mycrohyla carolinensis*) resembles the bleating of a lama. The pentadactyl giant frog (*Leptodactylus pentadactylus*) of Costa Rica hisses like a snake, while the giant frog (*Hyla crucifer*) really whistles. Another frog (*Paludicola fuscomaculata*) mews tenderly like a little kitten.

It would be an error to say that the voices of all the anurans are unpleasant. The songs of some tree-frogs (*Hyla*) and narrow-mouthed frogs (*Brevipectidae*) resemble the merry chirping of grasshoppers, the cries of guinea-fowls, or the frightened cheeps of chicks. Archy Carr, a well-known American herpetologist, writes that the songs of many tropical frogs are charming, full of optimism, and hidden meaning, and are more expressive than those of birds. Possibly, the scientist was carried away a little, but the voices of the American toad (*Bufo lentiginosus*) and some tree-frogs (*Hyla*) are extremely tuneful. They sound like little bells, reed-pipes or flutes. The voice of the cloud-forest frog (*Atelopus stelnzeri*) rings merrily during the nuptial season. Some fanciers keep frogs at home for their songs. The voice of the Japanese flying frog (*Rhacophorus reinwardti*) resembles singing birds. Good singing frogs are quite expensive in the markets in Tokyo.

The songs of anurans are addressed to the representa-

tives of the same species. They perform several functions: to attract females, to mark the borders of their territory, to ensure group contact, to demand freedom, to express aggressive intentions, or to warn of danger. Some frogs sing the "rain song" during the warm spring showers. Our edible frogs (*Rana esculenta*) produce six types of cries: one of them is sounded during the nuptial period, two are territorial ones, two are sounded for freedom and one as a signal of danger. The most significant cries are associated with reproduction. Their task is to ensure the meeting of partners. Sexual dimorphism (external differences between the male and the female) is not pronounced in the majority of frogs. It is easier to discriminate a male from a female and to make out the species of the animals by the sounds they emit. The calls of frogs are quite specific and prevent the possibility of hybridization.

The acoustic characteristics of the sounds have not yet been sufficiently studied. Nevertheless, it is known that the Californian newt (*Taricha torosa*) emits sounds of several types at a frequency of 1400-1800 Hz, our European newts (*Triturus*) and the Pacific giant salamander (*Dicamptodon ensatus*) squeak at a frequency of 3000-4000 Hz, woodland salamanders (*Plethodon*) generate sounds of about 5000 Hz, and the acoustic calls of the gracious salamander (*Ambystoma gracile*) are within the range of 400 to 7000 Hz. The duration of the acoustic signals of salamanders is rather short: from 0.04 s in the gracious salamander to 0.4 s in the case of newts. The call of a meridional West-Mediterranean tree-frog (*Hyla meridionalis*) comprises 30-40 pulses with a total duration of 200-600 ms. The interval between individual series of pulses fluctuates from 1 to 2 seconds. The cry of rivalry comprises only 3-4 prolonged pulses with a total duration of up to 1 second. The contact call is a series of brief individual pulses. The number of pulses in the series is

reduced in cold weather, while the intervals between the series increase.

The main frequency of the running (*Bufo calamita*), European variable (*Bufo viridis*) and the Sierra Nevada (*Bufo canorus*) toads is 1550 Hz. However, the females are never confused because they easily discriminate the value of the intervals between individual acoustic series from 30 in the European variable toad to 35-41 ms in the Sierra Nevada toad, and the total duration of the call from 0.5 in the running toad to 4-7 seconds in the European variable and Sierra Nevada toads.

Anurans emit quite low-pitched sounds: the palmate-footed frog (*Rana palmipes*)—from 100 to 2200 Hz, the common frog (*Rana temporaria*), the fire-bellied (*Bombina variegata*) and red-bellied (*Bombina bombina*) toads—400-600 Hz, the tree-frog (*Hyla regilla*)—2300-2500 Hz, the royal tree-frog (*Hyla arborea*)—2000-3500 Hz. Only some aquatic frogs generate high-pitched sounds. The nuptial calls of the clawed toad (*Xenopus laevis*) comprise ultrasounds at a frequency up to 80 000 Hz, and there is a clawed toad (*Xenopus ruwenzoriensis*) that generates sounds at 150 000 Hz!

The character of the sounds depends on the ambient temperature. The number of cries and the frequency of the pulses, generated by the running toad (*Bufo calamita*), increases during a rise of the temperature, while the interval between the cries and their duration is reduced in the case of the variable toad (*Bufo viridis*). The tree-frog (*Hyla versicolor*) generates 15 pulses per second at 16°C and 24 at 24°C. Orienting by the character of the nuptial song, females with a body temperature of 16 and 24°C unerringly pick out males with similar body temperatures.

The size of the animal affects the character of the emitted sounds: the bigger the animal, the lower the pitch of the sounds. The latter is observed when analyzing the

freedom cries of common male frogs (*Rana temporaria*) and the nuptial cries of the European variable toad (*Bufo viridis*).

During the nuptial period the amphibians are engaged in searching for a partner but they also jealously watch one another. The males of the running (*Bufo calamita*) and European variable (*Bufo viridis*) toads respond to the nuptial calls of other males and move in their direction. They unerringly recognize the voices of males of their own species and will not be fooled by incorrect imitation. But if a female has not been found by twilight, the unreasonable demands fade away and the males will be interested even in a rough imitation of the nuptial song.

The audible signals, produced by anurans, are not distinguished by great variety. As in other species of animals, they have been subjected to thorough selection during evolution. For example, the nuptial calls of males, who cry while being in a burrow, in the hollow of a tree, or in a surface nest, are usually brief and powerful sounds. It is difficult to localize these signals in space, but the females still find the males otherwise they would have died out long ago.

The communication and hearing systems of amphibians are far from perfect. The voices of the green (*Hyla cinerea*) and gracious (*Hyla gratiosa*) tree-frogs are not quite different, though they breed at the same time in the same water bodies, and the females sometimes confuse them. In order to avoid confusion the gracious male tree-frogs call out only when they are in the water, and the green tree-frogs sing their songs while staying ashore and climb up a bush or a tree to do it. This is the main guide for the female.

The males of many frogs and toads adjust their "songs" during the mating period to the "song" of their neighbour at the breeding ground. A soloist of the pseudocricket frogs (*Pseudacris streckeri*) will not stay silent if

after 30-50 ms of ending its call it hears the call of another male with a duration of 50-60 ms. It will not respond to a call of any other duration. A similar reflex is used in the formation of duets and chorus singing by other species of frogs. When two male panther toads (*Bufo regularis*) are neighbours, they coordinate their singing and form a harmonious duet. The common interval between the cries of each male increases almost twice in this case, because each singer, having finished his part, listens attentively to the neighbour's song and only then starts a new song.

Giant frogs (*Hyla crucifer*) compose duets, trios, quartets and even quintets. A leader may appear in the group of singing males. Quartets and quintets more often sing without a clearly expressed leader. To ensure coordination in the singing of 4-5 frogs each singer listens carefully to the songs of the partners and keeps to the order of priority. Senegal spade-footed frogs (*Kassina senegalensis*) make up singing groups of any number of animals without a leading soloist. Each animal sings for 2-8 seconds. Its singing evokes an immediate response in one or several frogs, and each animal occupies an exact place in the general chorus.

The olfactory analyzer is one of the major organs of sense. It has the form of paired sacs with folded walls interconnected with the oral cavity and the nostrils opening in front of the eyes. Thus, the entire amount of inhaled air is subjected to analysis. The amphibians have here a special compartment, which is characteristic only of terrestrial animals, namely, the Jacobson's organ, which is designed for the olfaction of food in the oral cavity.

Aquatic amphibians analyze aromatic solutions, while their terrestrial relatives must dissolve the odorous substance present in the air. To ensure this the olfactory cavity is supplied with moisture from numerous tiny glands. This complicates olfaction but not so much as it

had been considered only recently. Olfaction is necessary when hunting, during the mating period for discriminating their own species, for determining their sex and age, for spatial orientation, and for organizing defence. Marking of the occupied territory by odorous substances indirectly indicates the advanced development of the olfactory analyzer. Olfaction is very important for urodeles and, apparently, for those without limbs. The behaviour of newts with a destroyed olfactory analyzer changes more than in the absence of sight and hearing.

The olfactory stimuli of tailed amphibians may cause a whole complex of behavioural reactions. For example, the scent of a predator causes a hiding reaction in salamanders and it may last quite long. If the animal scents the smell of food, it is stimulated to search for food. Scent can urge food activity. When frogs are systematically shown tiny mobile objects through the glass of the aquarium, it will just as systematically try to grasp them. It will take a lot of time for the animal to become convinced of the utter futility of its attempts. But, if an air jet, smelling of some known food, is directed into the aquarium, the hunting reaction will be immediately stimulated again.

Amphibians are unable to determine the location of the food by the water and air jets, bringing in its scent, but they understand that the food is somewhere nearby and search for it actively until they find it. A strong smell causes stronger excitation and, consequently, more active searching. The animal will determine correctly the location of the prey only when the distance to it is less than a centimetre. Orienting themselves by means of olfaction, the greenish newt (*Diemictylus viridescens*) and the tiger salamander (*Ambystoma tigrinum*) can find and eat an immobile prey. Olms (*Proteus anguinus*), as it had been mentioned earlier, find and eat fish spawn and also unused spermatophores. The yellow lungless salamander (*Desmognatus fuscus*) and its closest relatives, protecting

their spawn, detect and eat unfertilized eggs by means of olfaction. Anurans also use scent when hunting. For example, the leopard frog (*Rana pipiens*) and the running toad (*Bufo calamita*), sensing an attractive smell, turn toward it and make grasping movements with their mouth.

Larvae also possess olfaction and utilize it quite actively. Larvae of the spotted newt (*Triturus vulgaris*) perceive olfactory stimuli on the third day of life. A strong olfactory stimulus can frighten the larvae on the fourth day. The larvae use scent in searching for food after 9-12 days. The larvae of the European common toad (*Bufo bufo*) perceive a signal of danger – the secretion of special substances into the water when the skin of an adult toad is wounded, or their larvae and even the larvae of some other species are wounded. The wound is inflicted more often by the predator's teeth and, if a "frightening substance" is perceived, it means the predator is nearby and it is best to run away before it is too late.

The majority of amphibians use scent to find their home and territorial property. Olfaction is most important for blind salamanders. Wandering in underground water bodies, the olm (*Proteus anguinus*) orients itself by the traces of its own chemical markers, which it secretes on the substrate, and by the traces of other olms. These markers stay good for at least five days. A female, looking for a male, orients herself by his traces. A male recognizes all its closest neighbours by their scent. It remembers well who of them is especially aggressive. It will never invade the latter's territory, but it is quite indifferent to the presence of strange olms in new surroundings. It is necessary to learn to orient oneself by means of olfaction. It is a fact that young olms are unable to use it.

Terrestrial amphibians also mark their territory. The red-backed salamander (*Plethodon cinereus*) confidently

recognizes its marks and those of representatives of its own species, distinguishing them easily from the traces of other salamanders. Red-backed salamanders, wandering in the vicinity of their estate, carefully smell around. They know immediately if they trespass on the property of another red-backed salamander and leave it with haste. However, they do not object to hunting on the territory of salamanders of other species. The animals defend their own territory only from representatives of their own species. Meeting another red-backed salamander on its property, the owner immediately excretes a drop of faeces. Faeces are used in the world of salamanders as chemical messages or credentials, confirming the rights of ownership over a certain territory. Olfaction is also used for orientation in a strange locality. The Mexican coastal salamander (*Stereochilus marginatus*) finds its spawning ground during the breeding season by scent. Our edible frogs (*Rana esculenta* and *Rana ridibunda*) as well as the red-bellied toad (*Bombina bombina*) turn in spring to olfaction with the same aim. The Southern leopard frog (*Rana utricularis*), on reaching the point of bifurcation in a T-shaped labyrinth, defines correctly the side which smells of pure distilled water, and the side with the aroma of brown-yellowish pond water, which is pleasant to it, and confidently takes that turn.

Amphibians can recognize entirely foreign odours. The Mexican coastal toad (*Bufo valliceps*) can be trained to find a cool and moist shelter in a T-shaped labyrinth, orienting itself by the odours accompanying water, i. e. the odour of aniseed or geranium oil, cedar balsam, benzaldehyde and creosote. This wide range of odours has been found intelligible by the toad.

Amphibians recognize familiar "game" by its scent. An experiment was set up, in which there was competition between different visual and olfactory stimuli. An extract of earthworms has been put into an aquarium

with crested newts (*Triturus cristatus*), a familiar food that was their preferable diet. The scent of the familiar "game" stimulated the animals. The newts started to search for it, smelling carefully the bottom and making grasping movements with their mouths all the time, but paid no attention to black squares, moving outside the glass of the aquarium, the sizes of the squares being from 10 to 300 sq.mm. They did not resemble worms, whose smell was so delicious. Even insects attracted their attention very little. At any other time, when there was no specific scent in the aquarium, both insects and moving squares were attacked systematically by the hungry animals. A similar experiment with edible frogs (*Rana esculenta*) showed that the scent of bugs, normally avoided by frogs, made them ignore flies. Apparently confused by the scent, they took the flies to be bugs.

Amphibians actively use taste receptors. The taste buds are within the tongue's epithelium and in the mucous membrane of the oral cavity. The buds are quite large in the olm (*Proteus anguinus*). As in other animals, they react to four types of flavouring substances: sweet, bitter, sour and salty. Each taste bud reacts to 2-4 types of substances. By means of the taste analyzer a frog unerringly discriminates a beetle in a strong chitinous armour from a dry bilberry leaf.

Urodeles are richer in analyzers than terrestrial animals. Aquatic species have preserved the lateral line organs, which they have borrowed from fish, using them only for orientation in the water. They react to the relatively rare vibrations in the water, caused by the motion of aquatic animals, performing the function of remote tactile receptors, and may be used for active location. Its principle of operation is as follows. The amphibians create wavelike vibrations in the water during locomotion. These pressure waves, propagating in front of the swimming animal, travel considerably faster than it. They

are the first to reach any objects, reflect from the latter and, returning back, are sensed by the organs of the lateral line. Active location of the surrounding space replaces vision completely in fishes and amphibians, who inhabit turbid water and move about at night. Scientists have noticed a long time ago that accidentally blinded fishes can detect mobile and immobile objects, grow and develop very well and are in no way inferior to their sighted relatives.

The perceiving elements of the lateral line are the hair cells on the surface of the skin. Their main function is to determine the direction and speed of the water flows. They are assembled in groups of 3-8 or 18-20 in newts, 20-40 in salamanders. Surrounded by basal and epidermal cells, they form a neuromast with a high and flat outgrowth, a cupule, with the sensitive hairs in its base. The sensitive neuromasts are arranged in groups, but not more than six in each group. Only the tropical clawed toad (*Xenopus laevis*) sometimes has as many as 10. The number of these groups is greater on the head and in the front part of the body than in the rear. During motion of the water, the somewhat flattened cupule bends perpendicular to its wide side. Each of the two nerve fibers, approaching the neuromast, transmits information to the brain only when the cupule bends in one of the two possible directions. Thus, the neuromasts in the groups are oriented in different directions and the brain receives highly accurate information on the location of mobile objects.

The neuromasts form three lines on each side of the head. One runs along the mandible, and the two others begin behind the eye and run to the nostrils and further to the tip of the face. Three parallel lines, running along the whole body, start behind the gills (or the spot where they ought to be). Nevertheless, some minor deviations occur. For example, on the head of the elongated dwarf siren

(*Siren intermedia*), the two upper lines converge, forming a sensitive field.

The organs of the lateral line are well developed in such typically aquatic urodeles as the mud puppy (*Necturus maculosus*), salamanders (*Amphiuma means*), sirens (*Sirenidae*), while in the European cave olms (*Proteus anguinus*) and the aquatic cave salamanders (*Hydromantes gormanii*) they are even hypertrophied, evidently to compensate for the loss of vision. The spotted (*Triturus vulgaris*) and crested (*Triturus cristatus*) newts, who spend the greater part of their life ashore, use them to locate small amphipods, but only from a distance of 1 cm, which indicates the low sensitivity of the analyzer. The organs of the lateral line occur only in the larval period in the animals, which have left the water habitat forever, for example, the lungless salamander (*Desmognathus*), the black Alpine salamander (*Salamandra atra*), the fire (*Salamandra salamandra*), cave (*Hydromantes gormanii*) and red-backed (*Plethodon cinereus*) salamanders. The larvae of the clawed salamander (*Onychodactylus fischeri*) in the Far East of our country possess the most powerful organs of the lateral line. They are found also in the larvae of anurans, but they disappear after metamorphosis. Our spotted and crested newts, having migrated in spring to the water, use the organs of the lateral line quite actively. After spawning they return to terrestrial life and the neuromasts submerge deep into the skin and the canal so formed is filled with mucus. This canal in salamanders is closed entirely by epidermal cells, which later convert into a horny tissue. In the dwarf siren the neuromasts are not subjected to any considerable changes because they are reliably protected against drying by a cocoon during summer hibernation.

Zoologists suspect that the organs of the lateral line may inform their owners of the water temperature and on the appearance of electric fields of biological origin. The

existence of highly sensitive galvanometers has been definitely detected in many marine and freshwater fishes, but their existence in amphibians is only an assumption today.

Family Troubles

The breeding season is the most violent time in the life of amphibians, who are usually so quiet and unobtrusive. Many of them pay absolutely no attention to their offspring but are extremely active during the nuptial play. Others, on the contrary, exhibit extreme devotion. Urodeles, as a rule, are thoughtful parents. Unlike our northern frogs, they do not spawn all the eggs at once, but do it in small portions, build nests for the eggs in thick vegetation, and even roll up the eggs in leaves. The male or both parents together quite frequently guard their offspring.

All the emotional ardour is spent during the nuptial period to attract a partner, to make the latter long for offspring, to synchronize its behaviour. This is how it occurs with the Siberian land-salamander (*Hynobius keyserlingi*).

The land-salamanders go to the water when spring comes to the North, and they have no time to spare. When the water warms up, the female begins to search for a well sunlit spot, which is not very deep in the water. It finds a reliable bunch of algae or a snag near the water surface (it will be warmer there for the little ones) and clings to it with her feet. Then she starts to curve her body and wag her tail in a wave-like fashion. The males rush up in response to this peculiar dance and start a merry dance in a ring around the female. The dancing males swim up to her in turn and touch the bottom part of the female's belly with their snouts. When assured that the males have surrounded her, the female spawns paired

sacs with 40-125 eggs in each and attaches them to the snag or plant where it had "danced". Her functions end and she yields her place to one of the males, who attaches a spermatophore, a paired package with spermatozoa, to the egg sacs.

The males are the leaders among Semirechensk salamanders (*Ranodon sibiricus*). Finding a deep niche under the stones, or a good snag, it sticks there a paired sac of spermatophores and begins to dance. Other males join in. The female, attracted by the dances, appears, finds the spermatophore and attaches a paired egg sac to it.

This method of breeding is called external fertilization. It is not characteristic of urodeles. Beside the land-salamanders, only large salamanders (*Cryptobranchidae*) practice it. Internal fertilization is a characteristic of all other urodeles.

The reproduction of newts starts with the search for suitable water. Naturally, tastes differ widely. Yakutsk land-salamanders prefer well-warmed shallow waters at the banks of lakes and rivers or flood plains with the residue of dry stalks of last year's vegetation, that are used by the females for attaching their egg sacs, while the European land-salamander likes more sphagnum-sedge bogs. The spotted (*Triturus vulgaris*), crested (*Triturus cristates*) and palmate (*Triturus helveticus*) newts choose large, abundantly vegetated but shallow water bodies. The Semirechensk salamander (*Ranodon sibiricus*) breeds in mountain springs and small rivers.

Amphibians need suitable weather for breeding. When the water is warm enough, the males are the first to dive in and begin to search for a reliable shelter. It may be a stone, a snag, a thick bundle of algae. When the choice has been made, the male marks its plot, pressing with its cloaca to the nearest stones and plants. The odorous "frontier posts" have two purposes. Firstly, males never linger on foreign territory, though its owner does not

reveal any aggressiveness. Secondly, the marks are necessary to attract the females. When the latter appears, the male begins to wag its tail, which the females regards as the most hospitable invitation.

Having found the marks and making sure of the goodwill of the host, the female becomes animated, turns her head excitedly, opens and closes her mouth, makes sharp turns and secretes strongly scented substances that are most attractive to the male. The host of the underwater "estate" hastens to make the acquaintance of the lady-guest, sniffs her all round, demonstrates his tail and starts the nuptial dance, which consists of certain motions of the body and mainly of the tail. The male circles around his beloved, following her closely, stands almost upside down on his head, and then wags his tail violently, showing his strength. The female stands still each time, as if she is sniffing him. The courtship dance lasts for about 2 minutes, and then the male stops dancing. He becomes now the leader and the female follows her spouse closely, charmed by his wagging tail and trying to reach its tip with her nose. When she manages to do this, the male stops, lifts his tail and deposits a spermatophore. The female grasps it with the lips of her cloaca. The nuptial act has been completed and the spouses may separate. The courtship dances may be performed on the bottom, on underwater plants and even in the water, but the male must feel "hard soil", even if it be a green leaf, to deposit the spermatophore. The whole procedure lasts from 40 seconds to 3.5 minutes.

Mole salamanders (*Ambystoma talpoideum*) perform a similar dance. When the male finds a female, he approaches her, hits her head and slides along her body, until he reaches her cloaca. The female, in turn, moves her head toward the cloaca of the male and both begin to push one another with their heads, making one or two circles, as if waltzing. The male is the first to break away

from his lady, and she slides with her head toward the tip of his tail. Wagging his tail in wave-like motions and accompanied by the female, the male moves slowly ahead, and it continues to do so for several minutes. Finally, the female gets sick and tired of it. She accelerates her motion and hits the male's cloaca with her head. He stops immediately, deposits a spermatophore and continues motion. The attention of the female is now attracted by the spermatophore. She sniffs at it, slowly covers it with her belly until it touches her cloaca and grasps the whole spermatophore or at least its top with the lips of her cloaca. She immediately loses all interest to the male and goes away.

However, the dance may be repeated up to seven times and continue for half an hour without final fertilization because successful grasping of the spermatophore at the very first attempt is rare. Other males sometimes join in the nuptial dance of the couple. If one of them manages to squeeze in between the tail of the first courting partner and the snout of the female, he begins to dance with the first step and the female dances then with him. Many spermatophores are lost during courtship because the female takes no notice of them if they are deposited during the wrong steps of the dance.

Not very many urodeles are so peaceful during the nuptial period as the spotted newts (*Triturus vulgaris*). The olm (*Proteus anguinus*) selects for breeding a plot with a suitable system of shelters under stones or in crevices in the rocks, which he marks very carefully. The plot may be very small, only 20-25 cm in diameter, but the host is always on the alert, continuously patrolling its borders, and if he detects a transgressor, beats him up. He rams the unwelcome guest, beats him with the tail, bites and inflicts wounds.

Tramps are also encountered among urodeles. They never have an estate. They always go looking for a female

because they are too impatient to wait till she appears by herself. Brook newts (*Taricha rivularis*) wander in small rivers and brooks. They go upstream and carefully sniff around to find a female.

Scent is extremely important for all the urodeles during the nuptial period. It allows the spouses to make sure of their choice, and the aquatic amphibians use it to find one another. On meeting a female, the males of newts, salamanders, olms carefully sniff at her. The females are more trusting and, if they see that the males have not lost interest after sniffing at them, they are ready to participate in the nuptial plays. The cloacal glands are the source of scent in all the urodeles. In addition, chin glands function in this capacity in male newts and lungless salamanders, while brook salamanders have small glands, suspended from the upper lip like little moustaches. The males touch the scenting spots on the females during the nuptial plays and leave their own scenting marks on the female's body.

Visual stimuli are of great significance for the development of nuptial behaviour, especially in terrestrial species. A male fire salamander (*Salamandra salamandra*) is ready in spring to attack any moving object, whose size resembles that of a female. Animals, which breed in water, are also not indifferent to visual impressions, and it is not without reason that male newts put on their finest nuptial attire at this time.

The organs of the lateral line are extremely important for blind salamanders. They allow the olm to locate the female exactly and not to make the mistake by putting his tail to her snout. She makes sure that she has met with a male by his scent. Even males with eyes react to a specific vibration of the water. It may even confuse them, and they will approach vibrating objects, having nothing in common with a female.

While depositing a spermatophore, the males of many

salamanders clasp the female with their legs, as if to hold her to the spot. This is not easy because the female is extremely slippery. For this reason many amphibians develop rough callosities on their toes, that have been called nuptial spurs. The spurs develop on the hind limbs of the red-spotted salamander (*Nothophthalmus viridescens*) and its relatives. The males of the fire salamander (*Salamandra salamandra*) and fin salamander (*Pleurodeles waltli*) clasp the female from underneath. The spermatophore is deposited on the female's body and the male moves it with his toes closer to the cloaca. Claspings play an important function. It assists the male to make sure that the female is ready for reproduction. Otherwise, she will not allow the male such liberties. She breaks free and swims away, so saving the male a ready spermatophore.

The behaviour of the male depends on his internal condition. He can repeat the entire ritual of courtship 7 times running and the female will participate in every new dance. The animals are so carried away that they will not surface for fresh air. The males are more active and, consequently, suffer more from the lack of oxygen, but they endure it selflessly, never stopping the nuptial ritual. The females are not so firm. They are the first to surface, which means an end of the romantic rendezvous.

The courtship play of a quick and simple dance is repeated many times by our newts and the Mexican land-salamander (*Dicamptodon ensatus*), and is followed each time by the deposition of a spermatophore, so increasing the probability that the female will finally take one of them. The dance is not repeated so many times by the tiger salamander (*Ambystoma tigrinum*). The females force the males to deposit a spermatophore at the end of each dance, but they take only one of them. And finally, the Jordan woodland salamander (*Plethodon jordani*) dances slowly, with many steps, but deposits only one

spermatophore which is never lost, and this is the end of the rendezvous. The males sometimes fight with one another for the female. There are also other ways of getting rid of a rival. The males of the tiger and Jordan salamanders can imitate female behaviour, making the rival to deposit useless spermatophores until his stock is fully wasted. This method is quite efficient if we recall that a male Jordan woodland salamander quits after depositing the first spermatophore.

In the case of external fertilization, the spermatozoa from the spermatophore enter the mucous egg sac and fertilize the eggs. If fertilization is internal, the spermatozoa live for some time in the female's body. They are held in the cloacal spermatheca and enter the oviduct. Some of them penetrate into the glandular walls and remain there till the egg passes, entraining the spermatozoa with it. The spermatozoa, remaining after the passage of the last egg, perish.

The female lays the fertilized eggs in small batches. The woodland Alpine salamander (*Plethodon neomexicanus*) lays 5-12 eggs in underground shelters. Our newts wrap their eggs in the leaves of underwater plants. The female of the warted newt (*Tylototriton andersoni*) lays 2-3 eggs at an interval of 3-4 days between each laying and attaches them underneath floating leaves. It has been found that the marbled (*Ambystoma opacum*) and the engirdled (*Ambystoma cingulatum*) salamander hide their eggs in holes and pits that are later flooded with water. These tiny clutches, that are laid anywhere, are not guarded, as a rule. Some of them are found by predators but others have a chance to survive.

If all the eggs are deposited in one place, the amphibians guard the clutch. The nest of the dusky salamander (*Desmognatus fuscus*), dug out by the female in the silt or sand in a small cave, is a maximum of 0.5 m from the water and, therefore, its walls are always wet. It has no

exit and the female stays near the clutch for 2 months until the larvae appear from the eggs. The female covers the spawn with her body and stays there for the whole time to keep the eggs sufficiently wet even in case of long-term drought.

Dusky salamanders make sometimes collective nests. A third of them holds 2 or 3 clutches that are guarded by one female. The spawn survives better in guarded nests than in unprotected ones. This is because the females can defend their clutch against small predators, humidify the spawn and, due to the fungicidal property of the mucous secretion of the female, preventing the development of various moulds and microorganisms on the eggs. It happens occasionally that a four-toed salamander (*Hemidactylium scutatum*) comes across the nest of another female, drives away the hostess, eats up a part of her spawn, providing herself with food for the long period of imprisonment, lays her own eggs and stays to guard the double offspring.

The presence of the female is advantageous also for eggs laid in water. The yellow lungless salamander (*Desmognathus fuscus*) stays all the time near the clutch and drives away water beetles and other salamanders that devour spawn with pleasure. She moves her body continuously to develop a fresh water current that ventilates the clutch and eats the eggs that are contaminated with different microorganisms, thereby preventing infection and putrefaction of the others.

If the female lays the eggs on a territory defended by a male, then he stays on guard. Male hellbenders (*Cryptobranchus alleganensis*), big North-American amphibians at the beginning of September look for a secluded spot somewhere beneath an overhanging bank, in the crevices of rocks, or under big stones, where the female lays 300-400 eggs. It is not a rare case that several females lay their eggs in the same nest. Then the male takes care of

the offspring and stays in the nest for 2-3 months, defending it against enemies until the larvae emerge.

The females of olms (*Proteus anguinus*) lay about 70-80 big eggs. It takes about a month for the female to produce so many eggs. She lays them all over the territory of the male, attaching them to stones, or sticking them into crevices. When she has laid the last egg, the tired female stays with the male for some time and it seems that she assists him in guarding the offspring. However, she goes away very soon. The males stay true to their parental duty and defend the life of their helpless children for five months.

Some mothers pay more attention to their children. The marbled salamander (*Ambystoma opacum*) lays 50-200 eggs in late autumn in a small hole somewhere in the forest. The eggs develop rapidly but it is necessary that the hole be flooded with rain water. If the weather is dry, the hatching of the eggs is delayed till spring, and the female moistens the eggs with her dermal mucus.

The four-toed salamander (*Hemidactylium scutatum*) does not rely on rains during the reproduction season. She lays her 30 eggs somewhere in a damp place and moistens the clutch for two months with the mucus of her own body. When the larvae emerge, they search for at least a tiny hole with water, where metamorphosis is completed. The red-backed (*Plethodon cinereus*) and the seal (*Desmognathus phoca*) salamanders also lay their eggs on land, but their larvae manage without water. It is interesting to note that even sirens (*Sirenidae*) spawn on land though they live all their life in water and never leave it except for reproduction.

The most considerate parents are the tree salamanders (*Aneides lugubris*), who manage to breed offspring on the trees. The larvae have no gills and cannot swim. The parents guard the spawn and defend it actively, bravely attacking and biting any enemy, no matter whether it is a

beetle, a sparrow, or a human. The depth of such parental love becomes more evident if we recall that salamanders are weak and tiny creatures. Their body length rarely exceeds 10 centimeters.

Urodeles lay from 2 to 700 eggs. Some of the females incubate the eggs in their bodies. Very few larvae emerge in case of internal incubation. If suitable shelters are not available for the spawn of the female olm (*Proteus anguinus*), all the 80 ova remain in the ovary to develop. But only 2 larvae emerge, while the other eggs dissolve into a nutritious mass that the larvae feed on. The two larvae of the black Alpine salamander (*Salamandra atra*) develop in a similar manner in the mother's womb, where they swim in a yolk mass of the other eggs. No yolk mass is found in the womb of the fire salamander (*Salamandra salamandra*), inhabiting the Pyrenees, and the bigger babies devour their little sisters and brothers without any hesitation. The larvae have no ties with the mother in the oviduct. She provides them with nothing except shelter. They must extract even oxygen from the nutritious mass wherein they live and its amount is very little. This is the reason for the big gills in these larvae. Intrauterine development is a long-term process. The females of the fire salamander carry their larvae for about 10 months.

Viviparity is important under unfavourable environmental conditions. It is associated with life in cold water. Hence, the black Alpine salamander (*Salamandra atra*), who lives under considerably more severe conditions than the fire salamander (*Salamandra salamandra*), carries her offspring to an adult state, spending almost a year to do it. Only the mother can create a suitable temperature regime for her offspring, because she can travel quite easily, following the sun to warmer spots. Beside that, the black Alpine salamander is capable of some thermal regulation.

The larvae of urodeles develop without considerable alteration. However, cases occur when the metamorphosis is not completed. Such a larva continues to grow, becomes an adult and starts to breed, quite as usual. This feature is characteristic of axolotls—the larvae of the Mexican land-salamander (*Dicamptodon ensatus*) in aquariums. This may also occur under natural conditions, if the larvae live and breed in deep water that never dries up.

The ability to reproduce in the larval stage is called neoteny. The latter is widespread among *Ambystomatidae*. Some species of this family are represented in the wild only by larvae, but it has been possible to complete their metamorphosis in the laboratory. Thus, it became possible to learn their outward appearance at maturity. Neoteny is characteristic of representatives of other families. For example, olms and sirens are neotenic forms of unknown salamanders, who have completely lost the ability to reach maturity. Neoteny has developed to cope with unfavourable environmental conditions. It emerges sporadically in *Ambystomatidae* under sharp fluctuations of air temperature, low humidity, lack of shelters, or of suitable food.

Anurans follow their own habits. With a few exceptions they practise external fertilization. The young may not be able to achieve maturity during our northern summer. For this reason, they start reproduction at the first indications of spring, when snow is still found in the woods and the first thawed patches show on the banks of lakes.

The common (*Rana temporaria*) and terrestrial (*Rana terrestris*) frogs are the first to hurry to the water. When it is warm and sunny, they manage to travel almost 0.5 km, leaping merrily in the wet snow. The males of the common frogs are stronger and reach the breeding ground the first. It is different with the European common toad

(*Bufo bufo*). The male prefers to find a girl-friend far from the water, climbs up on her back and then she carries him to the breeding ground. The males of common frogs gather in the warm sunlit shallow waters of lakes in forests. They may number up to 25 per square meter and may stay there for 2-3 weeks, i. e. they stay in the water during the whole breeding period, emitting monotonous gurgling sounds all the time. The females, on the contrary, stay in the water for a short time, i. e. one or two days. They spawn and return to the forest.

Frogs have their favourite water bodies in each locality, where they reproduce every year. Scientists still do not know the method they use to find them. There is an assumption that they use for reference the odour of microscopic algae. It is possible that the tadpoles feed on them, and that their presence is an indication of advantageous conditions for the development of the eggs and larvae in this water. The choice of plot is a responsible moment. The largest bull frog (*Rana catesbeiana*), owing to his physical superiority over the rest of the males, possesses a territory, where the loss of eggs is minimal, because the water never overheats and there are very few leeches, who feed readily on ova.

Anurans reproduce once a year under the severe conditions of the northern climate and in the mountains, but not all the females, as their tailed friends, manage to participate annually in breeding: the energy losses are too great, especially if distant migration is required in search of suitable water. Southerners have other troubles. The advantageous time for the development of the offspring is during the rainy season. Inhabitants of tropical rain-forests are not limited by strict dates. Some of them are very fertile. The charming banana frog (*Megolixalus laevis*) of Cameroon lays 4-5 clutches a year. The disc-tongued frogs (*Discoglossus*) in South Europe propagate during the whole summer. They lay 5-6 clutches, numbering up



A singing male tree-frog

to a total of 6000 eggs. This means that the greater number of offspring perishes without reaching sexual maturity. The number of offspring is small when the survival is great. The female of the viviparous African toad (*Nectophryne occidentalis*) breeds only twice in her life, the total number of young in both litters being a maximum of 20.

Anurans recognize one another by the voice during the nuptial period. The song is a sexual and species indication. It is more difficult for frogs, who live under conditions where audible signals are impractical. The tailed frogs (*Ascaphus truei*), inhabiting fast and noisy mountain springs, can hardly hear one another and, therefore, they are voiceless. The male puts forward all his efforts to find a partner in the depths of his native spring. It is no

wonder that the sight and scent are well developed in these frogs.

The song of the males is important for the female in order to recognize whom she has encountered. The whistling (*Hyla crucifer*) and coloured (*Pseudacris ornata*) tree-frogs inhabit the same locality, spawn at the same time every year and in the same water bodies, but hybridization does not occur, though it is not difficult to achieve this in the laboratory. This is explained by the difference in the males' voices, which the females discriminate quite easily.

However, confusion is possible. The males of the North American green (*Hyla cinerea*) and Anderson (*Hyla andersonii*) tree-frogs sing songs that are very much alike. The brides easily recognize their fiances, but the females of the Anderson tree-frogs prefer males of the green frogs (*Hyla cinerea*). The offspring of mixed matrimony develop normally but remain sterile. Encountering a group of males, the female will not rush to the first one she meets. The royal tree-frog (*Hyla regilla*) picks the partner whose voice is louder and the longest song, which means the strongest and most powerful male. This guarantees healthy offspring.

The females also make the choice in other species of amphibians. Male bull frogs are the first to arrive at the breeding ground, which is divided by the individual males not very peacefully. Then they sit on their plots and wait for the arrival of the females. The females look for the bigger males, because the difference between the biggest and smallest ones can be three-fold. The females see from afar the males sticking out their snouts above the water surface and they look closely at them, while the owners of the territory pay absolutely no attention at them until the female makes a final decision and pushes her chosen one in the side.

The sex of the partner and the readiness to mate are

determined finally by direct contact of the pairing animals. The male easily discriminates by the width of the female's waist one who has already spawned from a female ready to lay eggs, and even another male. Sometimes the readiness to mate is demonstrated by intimidatory posturing. In addition, audible signalling also assists the male. If a male grasps a female ready to spawn, she keeps quiet obediently. A male or a female, who has already spawned, will respond to this familiarity by a special sound, which is sometimes very low-pitched but will certainly be perceived by sense of touch owing to the vibration of the signalling animal and so the male will release it immediately. In the European common toad (*Bufo bufo*) in the Far East the release signal resembles the cheeps of chicks.

If the toads travel to the spawning ground in large groups and the males encounter one another all the time, some of them emit release signal at each leap in order to avoid possible sexual assaults of other males.

Sometimes the males make proposals themselves. When the tree-frog (*Colostethus collaris*) finds a female, he begins to emit audible signals and tries to impress her with ritual postures.

The European common toad (*Bufo bufo*) is an other example. The male waits for a female going to the spawning water. It is all the same to him whether she is big or little, quick or phlegmatic. The main point is that she should be a toad. The male grasps her, climbs up on to her back, arranges himself comfortably and then she carries him to the spawning ground. The female sometimes struggles stubbornly for a long time in order to throw the male off her back, but even if she surrenders, it does not mean that the matrimonial agreement is signed. The female requires that the male should correspond to her at least in size. They may meet some other unmarried males on the way and if one of them is bigger, stronger and

quicker, then the luckless fiance will be thrown off the back of his beloved.

Undoubtedly, when choosing a male, the female must do so rapidly, because otherwise she might remain without a partner. North American green tree-frogs (*Hyla cinerea*) assemble daily in the evening in the spawning water. The males are the first to go into the water, clearing up relations with their rivals on the way. Having settled and becoming accustomed to the environment, they wait for darkness and begin to sing at about 9 in the evening. The females make their choice rapidly. The singing ends in 2 or 3 hours, indicating that each male has found a bride. The females lay their eggs during the night and then they all go to the trees to rest.

The choice is usually made by the females by secondary characters. The intensity of the sound, its frequency and the total duration of singing are of major significance. If it is difficult for the female royal tree-frog (*Hyla regilla*) to decide whose voice is louder, she chooses the one who started to sing the first and who continues his vocal exercises without prolonged interruptions. It is more difficult for the female frog (*Physalaemus pastulosus*). She estimates the male's size by the sound pitch in the second part of the nuptial call. The lower the pitch, the bigger the male. The females easily distinguish sounds of 200 and 260 Hz in the laboratory and go toward the lower-pitched call without any hesitation.

The colouration of the female is of certain importance for some males. The male European variable toad (*Bufo viridis*) prefers dark objects, while the European common toad (*Bufo bufo*) is attracted by blue-coloured ones. They like this colour so much that a blue disk of 3-5 cm in diameter is always preferred to a female. Amphibians pay little attention to the shape. Males of many species pursue and try to grasp even such objects as balls that in no way resemble amphibians.

The character of locomotion is more important. The males of European common toads (*Bufo bufo*) recognize their beloved ones by their gait. The males are always in a hurry during the breeding season and move around in short leaps. The representatives of the weaker sex, on the contrary, prefer a slow trot. It is hardly possible to make an error.

It has been mentioned that violent fights may start between males during the mating season. The winner takes the female. Big old male midwife toads (*Alytes obstetricans*) can pair with 2-3 females, while the young and weak ones may stay alone. The males are very jealous. When the tree-frog (*Hyla avivoca*) who owns a plot sees the approach of a rival, he immediately changes his cry and attacks the trespasser, pushes and grasps him with his legs. The fight may continue for about fifteen minutes. Bull frogs (*Rana catesbeiana*) start furious fights. The owner of the plot attacks the unbidden guest and, if the latter will not retreat, continues to approach him, making brief stops on the way. Then the owner jumps at the trespasser and grasps him by the chest. The boxing rounds follow one another until one of the fighters is defeated. The loser never starts the fight again. Unable to survive the disgrace of defeat, he dives deeper and tries to withdraw without attracting attention.

The fire-bellied toad (*Bombina variegata*) guards a territory with a radius of 0.5-0.75 m, and the red-bellied toad (*Bombina bombina*) stands on guard of a territory, whose radius reaches 1-1.5 m. The size of the plot depends on many things. The Far East tree-frog (*Hyla japonica*) occupies a plot of 9-25 sq. m in large water bodies, where there is enough space, but they are contented with a small estate of 0.2 to 2.0 sq. m in small water bodies, where there are many rivals. The little strawberry frog (*Dendrobates pumilio*) of Costa Rica takes a position on the leaves of herbaceous vegetation at

a small height above the ground. The males arrange themselves at a distance of 2-6 m from one another. A special song informs all the other males that this particular male has assumed possession of the given estate. If a neighbour wishes to check whether this territory is well guarded, the owner warns him by a special cry, but if the curious neighbour invades the guarded territory, the owner thrashes him soundly, compresses the trespasser by embracing him with one or two legs, or leans all his weight upon him. Females never experience such troubles. They may freely explore any territory.

The tree-frogs (*Colostethus trinitatus*) of Trinidad occupy territories of a maximum of 1 sq. m and defend them only during their vocal exercises. Before starting his love songs, the owner of the plot turns from light brown to black. He will not defend his plot from accidental trespassers, such as males in brown. Only black tree-frogs call forth a fighting response.

There are more than enough fighters among frogs. Tremendous toads and tiny tree-frogs fight furiously. If two singing male royal tree-frogs (*Hyla regilla*) find themselves within 50 cm from one another, they stop their love songs and sound a war-cry. Sometimes nothing more is required. In other cases hand-to-hand fights start and continue till final victory is scored by one of them. Compromises are never accepted.

Mexican frogs (*Centrolenidae*) utter a long and loud war-cry, frighten the enemy with peculiar abrupt vibratory movements, then attack each other and begin to fight in conformity with the rules of Greco-Roman wrestling. These little puny and slimy creatures possess neither teeth, nor claws or horns, but they are fond of fighting.

The breeding grounds of the coloured tree-frogs (*Hyla versicolor*) are sometimes rather crowded. A spare male sits next to the owner of almost every fifth plot. He sits

quietly, silent. He is forced to be quiet. The owner will never tolerate a singing male next to him. The spare male waits patiently and, if the owner goes away on some business, then the spare one immediately takes his place and begins to sing. Sometimes there are two spare males. When the senior owner leaves the territory, his place is occupied by the spare male No. 1, and No. 2 waits patiently until No. 1 goes away and only then does he dare to open his mouth.

If the size of the breeding ground is limited, spare males appear also among Australian toads (*Leptodactylinae*), American leopard (*Rana pipiens*) and many other frogs. The spare males are always on the alert and try not to miss any lucky chance. If the owner of the plot, for example, a male coloured tree-frog (*Hyla versicolor*) manages to attract a female and becomes quiet when he grasps her, the spare male immediately starts his love songs, even before the owners of the territory commence to spawn. The spawning process lasts for 4-5 hours in the case of coloured tree-frogs and the invading male gains a real chance to find his own female.

A male, who wants to be a father, must be very patient. American woodland frogs (*Rana silvatica*) come to the spawning ground simultaneously. The males go into the water immediately, occupy a plot near the bank and start to sing. The females are not in a hurry. They wait until the water warms up and the ova mature in their bodies. Impatient males begin to look for partners. It happens sometimes that he grasps a female who is not yet ready to spawn. The male will not leave his beloved one and waits patiently till she signals her readiness to spawn. The process is accomplished in 10-15 minutes but the embrace may last for four days.

Amphibians are extremely patient creatures. The Asia Minor frog (*Rana macrocnemis*), inhabiting Armenia, prefers to spend the winter in calm deep waters. But

sunny Armenia is poor in water bodies and many frogs spend the winter in the soil. These frogs look quite listless and apathetic, showing no interest in their environment or in one another.

Asia Minor frogs, who are lucky to find a water body for the winter time, behave quite differently. They preserve extremely high activity, even if the water cools down to 3-4°C. The frogs make up couples at the beginning of October. Single females will not be found in a water body at this time. The male, who has made his choice, embraces his partner with his forelimbs and it is not easy to separate them. The female spends the whole winter in the arms of the male, waiting patiently for the approach of spring and warm weather. But after spawning, the male turns his back on her.

Long marriage is widespread among the cloud-forest frogs (*Atelopus oxyrhynchus*) of Venezuela. The animals lead a settled life and possess large territories. The males begin to look for females long before the period of reproduction. When the time comes for breeding, the male is the first to go into the water and he waits there patiently for several days till the female joins him.

In order to induce the female to spawn, the male must evoke a nuptial response in her. Nuptial dances are used to this end. Representatives of the stronger sex of banana frogs (*Megolixalus laevis*), sitting on branches, stage merry concerts and dance to their own melodies, adroitly beating their snouts with their long hind limbs. The tree-frog-actors (*Dendrobates histrionicus*) of Colombia stage real theatrical performances. The nuptial plays are accompanied by mad chasing high in the trees, rotation on the spot, funny curtseys and bows, tender touches, pushes and embraces to the male's song full of mirth. A spacious stage is necessary for the performance and it is not without reason that the territory, occupied by the male, reaches an area of 180 sq. m.

A spawning mood is called forth in the females mainly by their being grasped by the males and the latter utilize this on a wide scale. Male tree-frogs (*Phyllomedusa*), American toads (*Bufo americanus*), red-legged (*Rana aurora*) and some other frogs emit a special audible signal as an order to start spawning. Sometimes that is all that is required. Long nuptial play is necessary for frogs who manage without grasping one another during the spawning process, as it is with tree-frog-actors (*Dendrobates histrionicus*).

It has been considered until recently that all anurans are characterized by external fertilization. Certain exceptions from this rule are known today. The microscopic East-African toad (*Mertensophryne micranotis*), whose size is only 22-23 mm, and tailed frogs have learned internal fertilization. Real copulation does not occur in other amphibians. During the spawning period the female simply lays the eggs in the water and the male pours a stream of spermatozoa over them.

Many troubles disappear when spawning is on land. There is no need to be in a great hurry. Fertilization of the ova is possible even several minutes after they are laid by the female.

Even when spawning in water, the eggs and sperm may be cast out separately. Male Australian tree-frogs (*Litoria verreauxi*) are very careful when fertilizing the eggs. They spawn at the bottom of a water body. Finding an appropriate place, the female attaches herself to reed stalks and lays small clusters of 20-40 ova. The male, who is attached to the female with his forelimbs, picks up each cluster of eggs, pulls it close to his body, fertilizes the eggs and shifts them into the hind limbs of the female. She performs a rotary motion from time to time around the vertical reed stalk, attaching the eggs to it.

Tailed frogs spawn in swift mountain brooks. They use internal fertilization because otherwise the stream would

carry away the spermatozoa, and, as a result, tailed frogs (*Ascaphus truei*) need only 50 eggs, which the parents hide under stones.

It is sufficiently humid in the tropical jungles, and the eggs are not threatened by rapid drying. The frogs can afford to leave the eggs on the ground, on the leaves of plants, or in underground shelters. The eggs of many species develop quite quickly, the embryo passes through the entire cycle of development in the egg and hatches as a fully formed shaped frog. In such a case the eggs are very big because they must contain a reserve of nutrients and water for the entire period of development.

The tiny long-fingered African frogs (*Arthroleptis stenodactylus*) lay their eggs in underground chambers. Their 6 mm eggs seem enormous because their own height is only 3 cm. Fully formed frogs with rudiments of a tail hatch out in 2-3 weeks.

The little frog (*Anhydrophyrne ratragi*), inhabiting South Africa, also manages without water. The female digs out a small hole and lays one or two dozen eggs enclosed in a thick capsule. Tadpoles hatch out 10 days later and after another two weeks turn into frogs and only then do they leave their shelter.

The tadpoles are usually more in need of water than the eggs. It is necessary, therefore, that the hatched larvae should finally reach water. For example, the Brazilian toads (*Leptodactylus prognatus*) behave as follows. They leave the eggs to the mercy of fate in small depressions in the ground. If it begins to rain 5 days after the eggs have been laid, then all will be well. These toads reproduce during the rainy season and, therefore, the hopes of the parents are usually realized.

Female pseudotoads (*Pseudophryne bibroni*) and their closest relatives, inhabiting the arid regions of Australia, hide their eggs under stones, in crevices in the soil, between small mounds, or in any place where water col-

lects during the rains. If it does not rain during the first few days, the eggs do not perish, because the male stays on guard, or, to be more exact, he visits them at night and moistens the eggs with the slime of his body. The process of development lasts 1.5-2 months and, when the rainy season begins at last, well-developed tadpoles emerge. The males, who like all the amphibians are sensitive to changes in the weather, sense the approach of rain and leave their offspring.

The clutch of a so-called oily toad resembles a gelatinous mass with the eggs inside. The female lays them just at the water's edge. When the time comes for the larvae to hatch, the gelatinous mass is already diluted and moistens the path to the water, so that it will be no problem for the young to reach the water.

Tree-frogs (*Phyllomedusa*) and frogs (*Hyperolius*) lay a gelatinous mass of eggs on the leaves of plants. Some of them prefer that the cradle of the young should be near the water, while others are not afraid to use a leaf at the height of a three-storey building. The hatched larvae stay on the leaf until the gradually thinning gelatinous mass enables them to reach a water body.

Tree-frogs (*Phyllobates*, *Dendrobates* and *Colostetus*) take care of their offspring themselves. Most often it is the father who stays near the clutch, but sometimes both parents do. The hatched larvae climb onto the humid backs of their parents and attach themselves there. The mother and the father carry them one by one to a water, which is located somewhere nearby in the trees. It may happen that suitable water body is not found in the locality and the search for it will last for 8-10 days. The larvae of these species of amphibians are well adapted to this kind of transportation. They have a thick skin, which protects the tiny creatures against desiccation and injuries. They have a flattened body, which permits them to crawl a little, a short and strong tail, which is the sole

means of locomotion, and eyes on the back of the body, which ensure forward vision.

Some male tree-frogs (*Dendrobates*) carry their larvae from one water body to another. The idea of moving to a new apartment is to save their offspring from hunger.

Some frogs build nests for their offspring. The smith frog (*Hyla faber*) builds a small bath of mud and clay somewhere in shallow waters. The female takes the mud with scoop-like discs on her front limbs and makes a little dyke on the bottom of the water. She levels the space inside the dyke with her belly and chin until the dyke is raised above the water surface. The nest is thus separated from the rest of the water, and its maximum diameter may reach 30 cm. The male does not participate in building the nest. The hatching tadpoles spend their childhood in the parental bath, remaining inaccessible for fishes and other underwater predators.

The Brazilian tree-frog (*Hyla resinificatrix*) builds a bath for her offspring on a tree. When she finds a suitable hollow, the female seals all the slots with resin and coats the inside walls with it in order to make the hollow waterproof. The female then waits patiently until the tropical rains fill the bath. The tree-frogs avoid hollows that have been flooded earlier, because rotting has started therein and such water is no good for the young. Rare frogs (*Rana ishikawae*) reproduce in the hollows of trees growing near the shores of the Japanese islands of Ryukyu and Okinawa. The parents selflessly defend the family bath against the invasion of other frogs.

The purpose of the frog's nest is to safeguard the eggs against desiccation. The most original nests in this sense are those of the South-American toads (*Paludicola*), built of foam on the water surface. The foam protects the eggs against direct sunlight and desiccation and creates ideal conditions for supplying them with oxygen. If spawning is to start during hot dry days, the toads build their nests

on the bottom of dry pools in the hope of rain in the near future, but if there is no rain, the tadpoles are satisfied by the moisture in the nest. Some toads (*Pseudophryne australis*) build their foamy nests only on the ground. One or two males assist the female in building the nest. The outside layer of foam protects the larvae against desiccation and enemies without preventing ventilation of the nursery.

The moustached toad (*Leptodactylus mystacinus*) of Paraguay digs out small holes under stones to make similar nests. If the tadpoles emerge at the time of rains and big pools, they go into the water. But the eggs may perish if they are flooded by early rains. The white foam excellently protects the embryos against superheating. When the ambient temperature rises to 30.1°C, it is only slightly above 30.8°C in the centre of the nest, while the water heats up to 35.5°C. Such a high temperature is lethal for the embryos.

The female flying frog (*Rhacophorus schlegelii*) of Japan finds a suitable partner, allows him to climb onto her back and goes to the water, looking for steep banks. The male sits astride her back while she works all night in order to dig out a large burrow, where she spawns and surrounds the eggs with a foamy mass. The foam becomes progressively more fluid and drains to the water body, carrying the tadpoles with it. Wood flying frogs (*Rhacophorus*) build their foamy nest in the leaves, overhanging the water. The banana tree-frog (*Hyla nebulosa*) attaches foam-coated clusters of eggs to the underside of banana leaves.

The tree-frogs (*Phyllobates*) of the Antilles lay their 15-25 eggs right in the nest, which is a bag filled with liquid. The considerate mother attaches it somewhere in a secluded place. The tree-frogs spend their brief childhood in this aquarium. Aeration in the bag is much worse than in the foam and the tadpoles suffer from a lack of oxygen.

The tadpoles press their tails to the walls of their shelter to make up for the deficiency of gill respiration.

Leaf-frogs (*Phyllomedusa*) build hanging leaf nests. Carrying a male on her back, the female takes off on her dangerous wedding trip high up in the trees. When she finds a suitable branch at a height of 1-7 metres above ground level and overhanging the water, the female suspends from it by her forelimbs, while her hind limbs roll up a tube of leaves around her belly, where she lays small clusters of 300-600 eggs. If the nest is too small for all the eggs, she makes a second one. The male sits astride her back all the time and does not participate in building the nest. When the tadpoles emerge from the eggs, they drop into the water where their metamorphosis is completed.

The tree-frogs (*Phyllomedusa hypochondrialis*) lay considerably fewer eggs, only about 80-100. In addition, the female lays about 300 egg capsules in the hanging nest without embryos but filled with liquid. This reserve supplies the tadpoles with water during the entire period of development. The predilection of many frogs and toads for building nests is more often associated not with deficiency of water but with the lack of oxygen therein. Oxygen is deficient for the development of the eggs in warm water with an abundance of rotting vegetation. Hence, the necessity for cunning.

Anurans lay rather small eggs. The European midwife toad (*Alytes obstetricans*) lays her eggs on the ground in the form of two strings, in which 20-50 ova are arranged quite far from one another. The male assists the female in expelling the eggs. He grasps the strings with the toes of his hind limbs, pulls them out and entwines them round himself. A very active male can get eggs from 2-3 females. The midwife toads are entirely terrestrial animals and the development of their eggs continues for several weeks, while the father patiently carries the burden on his body. The eggs do not suffer because the multilayer envelope

encapsulating each one, protects it against drying and, beside that, it is possible for them to obtain fresh water by sucking it out of the father's skin. When the time comes for the larvae to emerge from the egg, the father repairs to a water body and, when the progeny is shed into the water, frees himself from the empty strings.

The back of the Surinam toad (*Pipa pipa*) is an excellent cradle. It is covered with wrinkles and folds, making deep (almost 15 mm) cells. The corneous layer of the skin and the glands in the skin on the back disappear during the breeding period. The spawn is laid in water. The male, as is customary in anurans, embraces the female from behind. The big cloaca of the female evaginates and turns onto her back. The spawning couple takes an upside down posture, the female squeezes out 1-5 eggs, the male relaxes his embrace so that the eggs can slide down between his belly and the back of the female. Now he grasps his partner tighter and presses the eggs into the swollen skin on her back.

The spawning process lasts for many hours because the male must accurately arrange about a hundred eggs. Several days later the walls of the cells acquire a hexahedral shape that makes them look like a honeycomb and the skin encloses the eggs on all sides, leaving only a small hole on the top. The extending upper part of the envelopes hardens, forming an operculum over each cell. The partitions between the cells and the underlying skin are rich in blood vessels that supply the eggs with oxygen and moisture and, probably, with food. The eggs increase their weight by 15 per cent toward the end of development. The *Pipa pipa* needs 80-82 days for the growth of 40-120 offspring. The cells open and the young emerge from their cradles. The skin on the back regenerates and the female is ready to become a mother once again.

Marsupial frogs (*Gastrotheca marsupiata*), like kangaroos, have a brood sac. It is arranged like a rucksack

on the back with the slit at the bottom. The brood sac of pygmy tree-frogs (*Gastrotheca pygmaeum*) is formed by two longitudinal folds that fuse together over the back. The egg sac is on the belly of the frog (*Gastrotheca orophylax*) on the Amazon slopes of the Andes. The skin, forming the sac, changes its structure: loses its poison glands, chromatophores, and the keratin resolves. The skin grows tender and enriched with vessels. Nipples grow in the sac of the river-bamboo frog (*Gastrotheca riobambae*) in order to supply oxygen into the sac.

During nuptial plays the males stimulate the females to spawn, pushing them with their hind limbs in the brood sac. The female's cloaca, as in the *Pipa pipa*, turns up on her back, that helps the male to push more than 200 big eggs into the "rucksack". The larvae are able to emerge themselves but the mother tries to facilitate this procedure and, using her hind limbs, extracts the young, simultaneously relieving herself of the dead and unfertilized eggs.

The male Australian tree-frog (*Assa dorringtoni*) has pockets in the inguinal region. The eggs develop on the ground and the emergent larvae crawl into the brood sacs of their parent. The big yolk sac provides them with sufficient food and allows the larvae to stay in the brood sacs till metamorphosis.

The females of some amphibians bear their progeny inside their bodies. In the case of ovoviviparity the large ova develop in the brood chambers, expanded oviducts of the female, owing to the nutritive materials they find there, while the mother supplies them only with water and oxygen. The larvae go through the entire cycle of development and fully formed creatures emerge into the light of day. Ovoviviparity is more common among African toads, inhabiting the arid zones of the continent. The tiny viviparous toad (*Nectophrynoides*) is capable of

keeping up to 15 toadlets in her body despite her small size.

The crying toad (*Nectophrynoides torneri*) of Tanzania is also rather small: the female is 32 mm long and the male is shorter by a whole third. The young are carried for 2 months and then quite microscopic creatures emerge. The female gives birth to three generations annually producing from 9 to 90 young ones.

An ovoviviparous leaf-frog (*Eleutherodactylus jasperi*) has been found recently in Puerto Rico. The eggs of these frogs stretch the oviducts and body skin to such an extent that they become transparent, making it possible to observe the development of the larvae.

The second type of intrauterine development is true viviparity. The eggs of the occidental viviparous toad (*Nectophrynoides occidentalis*) are tiny and poor in yolk, therefore the larvae need nutrition, which is supplied to them by the mother. The young feed for 9 months on the secretion of the uterine glands. The first 5-6 months of their life occur during the arid season, when their mothers dig themselves deep into the soil and hibernate. The young hardly grow during these hard times. The females leave their shelters with the first rains, begin to feed themselves and intensively feed their progeny. Under these conditions the young develop fully in 3-4 months.

The male Darwin's frog (*Rhinoderma darwini*) is the one to bear the offspring himself. Everything is just the opposite with these tiny creatures. Darwin's frogs live in water but the female lays her eggs on land in moist moss, and with this done her duties come to an end. The father, on the contrary, guards the clutch, but his interest in the spawn, at first sight, seems to be gastronomical. Looking carefully at the eggs, the male picks out one or two and takes them into his mouth. One might think that he has decided to dine on his young offspring. But you would be wrong. Instead of swallowing the eggs, the male takes

them into his vocal sac, where they continue to develop as if in an incubator.

The vocal sac of the father is quite small and he manages to put there a maximum of two eggs. However, the sac progressively expands and the father adds more and more eggs, and 10-15 days later the whole clutch is in the "incubator". The larvae, hatching from the ova, have a yolk sac with a considerable reserve of food, that permits the young to lead a careless life, swimming around in their close quarters. However, the nutritive resources are finally exhausted and the larva can do nothing but to press its back to the wall of the children's room and adhere to it at first with its tail and then with its back. As a result two layers of larvae settle inside the sac with their bellies toward each other. The skin on their back and tail has a peculiar structure, enabling them to extract oxygen and other nutritive materials from the father's blood. The tadpoles of this frog species spend their youth packed like cigarettes in a packet. When metamorphosis has ended and the tail fully reduced, the young lose all ties with the parent's body. They are no more in need of their father's support and the froglets are released one by one into the world, jumping out of his mouth and quickly hiding in the depths of the water.

The snub-nosed frog (*Rheobatrachus silus*) of Australia takes her offspring into her stomach because she has no vocal sac. The offspring live there until the end of metamorphosis. The secretion of the stomach is stopped or completely changed because otherwise the offspring would be digested as everyday food. The grown up froglets leave their nursery on their own initiative one by one or in small groups. When the prolonged childbirth ends, the mother can breathe with relief, which is understandable as she bears 20-30 young with a total weight of 7-8 grams, i. e. 65 per cent of her own weight. It should be borne in mind that she is unable to eat even a tiny morsel

during the entire carrying period. Sometimes the behaviour of the young is so intolerable that the mother really feels sick and tired of them and she disgorges them all at once.

A quite surprising example of parental care of offspring has been demonstrated recently to researchers by the little tree-frog (*Dendrobates pumilio*) of Costa Rica. It is very difficult to observe the behaviour of tree-frogs. It has been possible to look into the matrimonial relations of the little tree-frogs only when the latter were settled in a small greenhouse with tropical trees. When it is time to have offspring, the female starts to search for a "singing" male, who takes her to an earlier selected dry and horizontally arranged leaf. The female lays there 5-9 rather large yellow-orange eggs.

The parents don't guard the clutch but they visit and moisten it daily with dermal slime. Beside that, the mother eats up all the unfertilized eggs, thereby preventing decay of the others. When the tadpoles hatch out, the female carries each one on her back to the leaf axils of bromelin-epiphyte plants, that grow on the trunks of big trees. It is a pleasure to live in an individual water bath. The female visits one of her offspring once a day and lays 3-7 unfertilized eggs in its bath. The tadpoles feed on these eggs. Thus, the larvae grow on a diet of "red caviar" till they turn into little froglets in about two months. They stay in the bath until they eat up the reserve of caviar and then leave the hospitable leaf and start to search for food on their own.

These tadpoles are in close contact with their parents during the entire period of infancy. When one of the tree-frogs appears at the edge of the leaf axil, the tadpole surfaces immediately and begins to swim around vigorously so that it will be noticed. This is a signal for the adult frogs not to forget to feed it. It also warns the adults not to add another tadpole to this bath (two in one bath

means hunger), and the adult tree-frog must not bathe there because the water would turn dirty and the young would be unable to live there.

The small class of amphibians has developed many various and very unusual methods of reproduction. But we are still unaware of the methods of reproduction of many species of frogs, toads and salamanders.

Childhood

Childhood is said to be the best time of life. This is not so with young amphibians. Being left to the mercy of fate, the helpless larvae are exposed to the vicissitudes of life, and it is not without reason that the females lay from 5000 to 10 000 eggs annually to preserve the species. This is the number of ova deposited by the females of our edible frogs (*Rana esculenta*). The European common toad (*Bufo bufo*) fits 2000-3600 eggs in each of the two strings that she expels. About 99.5 per cent of the larvae and young amphibians perish usually long before sexual maturity. The red-legged frog (*Rana aurora*) of the Lake Marion in Canada lays about 800 eggs. Only 5 per cent of the hatching larvae grow up to small froglets and reach land. The others perish in the stomachs of trouts, newts, gracious salamanders, water bugs, dragonfly larvae and snakes. Another 4.5 per cent will perish on land.

Survival is most difficult for amphibians inhabiting arid regions. The climatic conditions make reproduction entirely impossible in some years. But about 1 per cent of animals grow to an adult state from eggs laid in favourable years. Thus, childhood is a period full of perils and only a few lucky ones manage to survive. This vitally significant period requires comprehensive discussion.

We shall begin the discussion from the very beginning, i. e. from the egg.

The ova are located in the amphibians in paired

ovaries, and, on reaching maturity, they are discharged out into the body cavity. Now they must enter the oviduct, which is a special tube, whose flared end, resembling a funnel, opens into the body cavity, while the other end goes into the cloaca. The funnel adheres to the cardiac bursa in sexually mature frogs. Heart contractions make the oviduct contract, dilate and suck in the ova. They are covered with mucous membrane while passing through the oviduct. The eggs may now be laid at any time.

The spermatozoa develop in the testes, which are large glands closely associated with the kidneys. Numerous small ejaculatory canals enter the ureters that have one special pocket each, a so-called seminal sac, where the mature spermatozoa are kept.

The mucous membrane of the egg swells rapidly in water and becomes impenetrable for the spermatozoa. The spermatozoa move around actively before this happens, look for eggs and penetrate their gelatinous walls. For this purpose they possess special enzymes that dissolve protein. The latter enzymes assist the spermatozoa to penetrate the egg's membrane. If the mucous membrane is dropped into sperm, it is digested.

The eggs of anurans contain very little yolk, which is concentrated in one place. The so-called yolk pole, which is the heaviest part of the ovum, is always turned downward. The upper, dark part of the egg is a screen, which protects it against lethal ultraviolet radiation. In the case of northern frogs it is also a light-absorbing surface, which heats well in the sun. This is helped to a certain extent by the external gelatinous membrane, which, on the one hand, focuses the sun's rays like a lens on the dark pole of the egg, and, on the other, prevents the egg from heat losses.

The eggs of southern frogs, which develop in the eternal glooms of tropical forests, do not need a light-protect-

tive screen and, therefore, they are colourless or camouflaged. For example, the embryos in the eggs of the leaf-frog (*Eleutherodactylus abbotti*) and in one species of midwife toads (*Hyperolius obstetricans*) are green.

The size of the eggs varies from 0.5 mm in the occidental swimming toad (*Nectophryne occidentalis*) to 25 mm in the marbled salamander (*Abystoma opacum*), and not every predator can harm such big eggs. Their development depends on the water temperature. The higher the temperature, the faster their development. The gracious salamander (*Ambystoma gracile*) needs 87 days for the development of her spawn in cold water at 7°C, 27 days at 12°C, and only 13 days at a water temperature of 20°C. When the temperature of the water rises from 8 to 18°C, the development of the spawn of an olm (*Proteus anguinus*) reduces by three times, i. e. from 6 to 2 months. However, such rules do not exist for northerners. The development of the larvae of the terrestrial frog (*Rana terrestris*), inhabiting areas with a moderate climate, takes 60-65 days, while it takes only 45-55 days at the extreme northern border of their habitat. Northern amphibians grow and develop in cold water even better than in warm. Larvae, collected in the Arctic on the Yamal Peninsula, developed at 5-10°C just like their relatives in water at 18-20°C, and gained weight even faster.

Wood frogs (*Rana sylvatica*) assemble for spawning in restricted parts of the water. They become very active and so warm themselves and raise the temperature of the local water. The developing eggs also warm themselves. The temperature inside a cluster of eggs of a wood frog is one degree higher than that of the water, and it is higher by 3°C in the case of the terrestrial frog. It is for this reason that the northern frogs spawn all their eggs at once. The situation is just the opposite one in the case of southern frogs, who must fight against overheating. The clutch of the bull frog spreads over the surface, actively evaporat-

ing water, and the temperature of the eggs drops below that of the water.

If the clusters are large, the respiration of the eggs is hampered, but the water in the North is rich in oxygen and the swollen membranes prevent the eggs from sticking together into a very tight lump, leaving between them a network of canals for free water circulation. The eggs of the common frog (*Rana temporaria*) find an additional source of oxygen by entering into symbiosis with microscopic algae that settle on their membranes in great numbers. This phenomenon is noteworthy because the egg membranes usually contain toxic substances that can kill any lodger. Ranidine, the poison of the egg membrane of the terrestrial frog (*Rana terrestris*), is so strong that it kills microorganisms faster than carbolic acid. It is not without reason that its dried spawn has long been used in folk medicine for curing erysipelatous inflammation.

The offspring of northerners had to adapt to low temperatures, and those of southerners to a hot climate. The spawn and larvae of the edible frog (*Rana ridibunda*) survive at a water temperature up to $+43^{\circ}\text{C}$ but perish at $1\text{--}2^{\circ}\text{C}$. The eggs of the terrestrial frog (*Rana terrestris*) remain alive even if the water is covered temporarily with ice, and those of the common frog (*Rana temporaria*) survive chilling down to -6°C but perish at $+24$ or $+25^{\circ}\text{C}$. A record of heat resistance has been set by the Philippine frogs (*Rana concolor*), whose spawn can survive a temperature up to 45°C .

The ovum divides when the spermatozoa penetrates it. The embryo begins to elongate and several days later one can see its head and flagellum, when it is almost ready to leave the egg. It is quite a hard task for the tiny embryo to escape from the egg as it is practically deprived of the ability to move actively. The strong membranes would have turned into a prison for the embryo were it not for

its special glands, whose secretion dissolves the membrane and releases an astonishing creature.

The young of all higher vertebrates, no matter whether they are born alive or hatch out of eggs, always resemble their parents. The anurans, however, usually appear very different when first hatched from the egg because they resemble their ancestors, fishes. They lack even an indication of limbs. Hence, the young tadpoles are called larvae who have to develop into little froglets.

Newly hatched tadpoles have a small body and tail, which is surrounded by a swimming membrane. However, they are still unable to move around and hang from nearby vegetation or the remains of the egg membranes, adhering to them by means of special suction cups. It is unnecessary for them to search for food because their intestine is full of residual yolk. The reserves of the Pacific giant salamander larvae (*Dicamptodon ensatus*) are enough for three months. The tadpole lacks a mouth at this time. By the time the reserve of yolk is exhausted, the mouth of the tadpole breaks through the skin, the break appears with lips around it in the form of a proboscis. The lips are rich in tiny horny teeth. Toads (*Pelobates*) have more than a thousand teeth. New teeth cut out when the old ones abrade. The tadpoles of anurans feed on microscopic algae, ooze, bacteria and vegetative detritus. The tadpoles of the leopard toad (*Bufo regularis*) slow down their growth if they are deprived of silt, containing microorganisms. Tiny animals enter the intestine together with the silt. The larvae of the edible frogs (*Rana ridibunda* and *Rana esculenta*) in the delta of Danube feed first on algae and plant residues. Then they eat live plants, also rotifers and various crustaceans, therefore, it is impossible to say that they are true vegetarians.

The larvae of anurans, like their parents, are predators. As they grow, they start to feed on larger prey. From 30 to 60 victims have been found in the stomachs of larvae

of the tiger salamander (*Ambystoma tigrinum*). The biggest ones had a length of 17 mm, a fifth of the predator's own size.

The larvae are usually not threatened by hunger, especially the vegetarians, but if there is some interruption in the feeding, they shift easily from a vegetarian diet to a carnivorous one, and sometimes turn into cannibals. The tadpoles of the pentadactyl toad (*Leptodactylus pentadactylus*), which live in water bodies in Costa Rica, feed mainly on the slow tadpoles of the marine toad (*Bufo marinus*), as well as on its own younger brothers and sisters.

The larvae of the fire salamander (*Salamandra salamandra*) are predators but they never sin by turning to cannibalism until they find themselves in corresponding conditions.

The young of many anurans, including the larvae of clawed toads (*Xenopus laevis*), feed only on food suspended in the water. When they lunch, they take water into the mouth and let it out through the gill slits, and the feed is retained by filtering devices. The water enters the oral cavity by lowering the floor of the pharynx. The mouth closes and the contraction of the floor of the pharynx forces the water through the gills.

The first feed of the tadpoles consists usually of the remains of the egg membranes. When they have eaten up the walls of their former shelter, the young start to search for food, which is quite easy because it is all around them in abundance. Hence, the eyes and ears are not developed yet at this stage. Only the organs of the lateral line are functioning. The olfactory organ, paired pits in front of the eyes, and the tactile papillae on the lips help in finding food.

The tadpoles are not dreaded by food competition. As it has been mentioned earlier, the larvae of lungless salamanders (*Plethodontidae*) possess quite a big yolk sac at

hatching out of the eggs, and at first they feed on it. The larvae differ greatly from one another in the intensity at which they use their resources. Some of them consume the yolk rapidly, grow very fast and soon start to feed independently. Others, on the contrary, use their food resources quite economically, grow slowly and start to hunt at a later stage. Brothers and sisters begin to differ in size from one another very soon after hatching, which means that they hunt different prey without competing with each other. Nevertheless, growth and development of the predatory larvae of the salamanders slow down if they are too congested. The herbivorous tadpoles of frogs and toads quite rarely find themselves in such a situation. Irrespective of their number, they are unable to consume more than 10-12 per cent of the nutritive resources in the water, while the larvae of salamanders can utilize 60 per cent of available food and then begin to starve. Hence, the density of the larvae of anurans may be quite appreciable, but certainly it is not infinite. When the maximum limit is exceeded, the development of the tadpoles is impeded and differences are observed between the larvae. Some of them develop slower than others. A daily and increasing difference may be observed in their size and degree of development. The age of the tadpoles is determined not by the number of days they have lived but by their stage of development, therefore, the water is now inhabited by larvae of different age.

One of the major laws in the life of young amphibians comes into effect: larvae of different age shall not be friendly. They are associated by very strange relations. The elder tadpoles accelerate their growth in the presence of their younger sisters and brothers, compelling the younger ones to slow their development. The size differences are thus aggravated. This situation can be reproduced easily in an aquarium populated with the larvae of common frogs (*Rana temporaria*).

Antagonistic relations between the tadpoles are biologically justified. They prevent an excessive increase in the number of amphibians. The reserves of feed in the water bodies of Meshchery, for example, ensure normal growth and development of the larvae of the terrestrial frog (*Rana terrestris*) till there are a maximum of 25 eggs per cubic metre of water. In this case 4-5 per cent of the larvae develop into froglets and go ashore. Only 1 per cent of froglets reach land if the concentration of the eggs increases to 60-70 in the same volume.

It was considered until recently that the processes, caused by high concentration of the larvae, are due to the accumulation of the products of their vital activity in the water. However, larvae, living under conditions of considerable congestion, developed poorly even in running water aquariums, from which their faeces were continuously removed, and where the concentration of chemical substances, capable of depressing the young, was negligible. Their brothers, who lived in more spacious quarters, developed normally, despite deliberate contamination of the water with faeces from other aquariums.

The response of the tadpoles to congestion changes with age. The tadpoles of the common frog (*Rana temporaria*) greatly depress and even cause the total death of the young larvae of the edible (*Rana esculenta*) and terrestrial (*Rana terrestris*) frogs, as well as those of the running (*Bufo calamita*) and European common (*Bufo bufo*) toads. The older tadpoles of the common toads depress the larvae of the running toad and common frog, the tadpoles of the tree-frog (*Hyla japonica*) depress the larvae of the oriental toad (*Bombina orientalis*). The most intolerant ones, the tadpoles of the common frog, gain greatly in growth and development if they live together with the larvae of the terrestrial frog. The metabolic products are more important than the psychological factor in interspecies relationships. They are characterized by great

specificity. The metabolites of tadpoles of different age depress or stimulate larvae only of certain species and at quite definite stages of their development.

The digestion of tadpoles has been studied very poorly. The food is retained in the digestive tract of the larvae of the cricket frog (*Acris gryllus*), woodland toad (*Bufo woodhousei*), bull frog (*Rana catesbeiana*), Caroline narrow-mouthed toad (*Gastrophryne carolinensis*) for only 30-100 minutes and is assimilated by 54-86 per cent. This readily explains why the tadpoles of the bull frog eat their own faeces. The ingestion of faeces greatly prolongs the time the food particles stay in the intestine and reduces the consumption of energy for disintegrating the food. The faeces are a vital part of the diet. When they were removed, for example, from the aquariums, the tadpoles of the bull frog lagged behind greatly in their growth.

The larvae of amphibians spend a greater part of their time in search of food. The tadpoles of anurans and their parents have much in common in their methods of hunting, therefore, when they leave the water in autumn, they are able to find their food independently. It is more difficult for the froglets. They have to transform themselves from vegetarians into carnivorous hunters. Luckily, the food behaviour of amphibians is innate. The young need only two or three days of training in opening their mouth and turning toward the prey. They frequently miss at the beginning and the prey manages to escape but soon everything turns well.

The larvae of amphibians are exposed to many perils, and the worst is drought. It may cause enormous and fatal losses to whole generations of salamanders and frogs. The larvae also have many enemies. Who would refuse a feast of tadpoles? The larvae of amphibians are devoured by fishes, predatory water insects and their larvae, newts, salamanders, frogs, snakes, birds and leeches. One species of crustaceans in the Alpine regions of Eu-

rope is an enemy of all young amphibians. The tadpoles of the common frog (*Rana temporaria*) suffer most of all from water beetles and their larvae. Poison is the only weapon of the young and their parents. The skin of a toad tadpole begins to produce toxic substances and they become inedible for predatory insects. If a school of tadpoles of the clawed toad (*Xenopus laevis*), agile (*Rana dalmatina*) or common (*Rana temporaria*) frogs is suddenly covered by a shade, the motor activity of the larvae increases sharply. Evidently this is an escape mechanism. The future froglets are capable of escaping enemies only after metamorphosis.

A lack of water is most dangerous for the young during their first days on land. The inhabitants of deserts and steppes have to be able to adapt in order to survive. For example, young spadefooted toads (*Scaphiopus*) can burrow into the soil from the very beginning of their life. Young prairie toads (*Bufo cognatus*) know how to burrow too, though not very deep, and can survive in the soil for about three months.

The tadpoles of anurans are sociable creatures. They need the society of their like to feel fully at home. The larvae of the midwife (*Alytes obstetricans*) and European common (*Bufo bufo*) toads grow and turn into toadlets faster in companies than in isolation. The young usually gather in schools, the larvae either push around at random, swimming in all directions, or, like fish, coordinate their actions. In the school of tadpoles of the clawed toad (*Xenopus laevis*) all the members keep strictly parallel to one another, though their heads may not always be directed toward one side.

Interaction between larvae by vision is possible at a distance which is equal to a double length of their body. It is performed in darkness by the use of the lateral line organs, but is only possible at a distance which is two times less.

The tadpoles somehow manage to recognize and remember one another. If newly hatched larvae are set into individual flasks, then they express no desire to gather in a school when let out into an aquarium after only one day. The larvae of one clutch have been kept in two groups for 24 hours and then would not merge when placed in a common pond.

The schools of tadpoles may be temporary or permanent. They feed actively and gather in schools in the daytime in the warm parts of the water body, while in the evening, when the water cools down, they disperse. Permanent schools are more stable. The tadpoles of the American toad (*Bufo americanus*) form groups that feed on dead and bottom organisms, or during metamorphosis. As a rule, the school is formed of larvae of the same age. In the case of the American toad it is always the larvae of one clutch.

The tadpoles control their body temperature by choosing the suitable temperature zone in the water. The larvae of the spotted (*Ambystoma maculatum*) and Texas (*Ambystoma texanum*) salamanders prefer a temperature from 13 to 29°C and run away from a warmer zone faster than from a cold one. The tadpoles dive to the bottom at night, because it is warmer there, but surface again at daytime to be nearer to the sun. This faculty of temperature control is manifested only at a certain stage of development. The larvae of the terrestrial frog (*Rana terrestris*), who have crossed the age threshold, become highly interested in the strip near the land, where the shallow waters are the warmest. They spend the light part of the day there.

The larvae of amphibians lack a swim bladder and they have to exert every effort to keep afloat. The young of some species have learned to hang from the water surface film, basking in the sun and digesting their lunch at leisure. For example, the funnel around the mouth of the

tadpoles of the horned toad (*Megophrys nasuta*) is quite big. The tadpole uses it to break the film of surface tension and then hangs vertically, staying immobile for hours.

The activity of the tadpoles sometimes saves their lives and renders considerable benefit to the other inhabitants of the water. Round pits, 1.5 cm deep and up to 6 cm in diameter, are found frequently on the bottom of ponds in North America and Europe. They are called "tadpole nests". When there is a lack of food, the larvae of anurans drop to the bottom and, searching for something edible, make circular movements with their body and actively working tail, thereby digging out nests-pits. The excrements of the tadpoles accumulate in these depressions, greatly facilitating the search for food by water beetles, mollusks, and small crustaceans, who feed on excrements and, like the tadpoles, suffer from the lack of food. If a drought occurs and the water bodies dry out, the "nests" enable the tadpoles to complete their metamorphosis before the water evaporates from the pits, while the other small fry may survive till the next rain.

The larvae need fresh water for their development, but the water should be neither acidic, nor alkaline, the latter factor being of major significance. Only a few species of Phillipine frogs (*Rana concrivora*) can live in water containing up to 1.5-2 per cent of salts. The waters in the Black Sea are approximately of the same salinity.

The tadpole breathes through three pairs of external gills during the first days of life. Then the internal gills begin to function. The water, entering the oral cavity, passes through it and, giving off the oxygen, flows out through the gill slits. The pump operates most actively in larvae who lead a settled mode of life. The tadpoles of the Australian lemon tree-frog (*Litoria citropa*) sucks in water and develops a negative pressure of 36 mm water column, while the larvae of the Australian stammering

toad (*Mixophyes balbus*) – 180 mm water column. The positive pressure, generated in the oral cavity to drive the water through the gills, may reach 240 mm of water.

While the internal gills develop, the external ones degenerate and finally disappear. The skin, especially the skin of the tail, which is rich in blood vessels, supplies the organism with oxygen.

A newly hatched larva is boneless. The body muscles develop together with the formation of the bony skeleton. Then the limbs appear. A septum, dividing the auricle into two parts, starts to grow in the heart, which has been a two-chambered one like in fish. The lungs and pulmonary veins develop. The tadpoles proceed to metamorphosis, whose aim is to transform the tadpole from the typically aquatic creature it has been until this time, into an animal, capable of living in an air environment. Some organs degenerate at this stage, while other develop just as intensively. Therefore, metamorphosis of the larvae of anurans is called necrobiotic.

The beginning of metamorphosis coincides with the appearance of the forelimbs, which break through the gill slits. After some time, joints develop in the limbs, the shape of the head changes greatly, the mouth grows bigger, and the eyes, which have been covered with skin, open up, the tail gradually reduces and the tadpole turns into an exact copy of its parents, being inferior only in size. The digestive track is reconstructed at this time, the gills and the organs of the lateral line disappear, the internal ear develops, the formation of the skeleton and brain is completed, the cerebellum and the cerebral hemispheres appear.

The tadpoles interrupt their feeding during metamorphosis, but they do not suffer hunger. The organs, that will reduce, primarily the tail, supply the organism with a sufficient amount of building and energy materials.

As a rule, the development is completed in one season,

but northern tadpoles are sometimes unable to complete metamorphosis and compelled to wait till the next spring. The childhood frequently lasts for 3 years in the case of tailed (*Ascaphus truei*) and bull (*Rana catesbeiana*) frogs in North Canada and of the midwife toad (*Alytes obstetricans*). The larvae of the bull frog can start metamorphosis only after growing to a length of 10 cm, landing is postponed for a long time if corresponding conditions are not available. A prolonged childhood, lasting for 2-3 years, is quite characteristic of salamanders, confined high in the mountains, and is typical of their underground relatives.

An opposite record has been set by frogs and toads, inhabiting the hot and especially the arid regions of the planet. Quite developed froglets hatch out of eggs laid 30 days earlier by the flat-bodied frogs (*Platymantis vitien-sis*), inhabiting the Fiji Islands. The tadpoles of the Namibian toad (*Bufo vertebralis*), who are in a hurry, complete metamorphosis in 21 days, the desert toads (*Bufo pentoni*) of Senegal manage it in 9-11 days, while the burrowing spade-footed toad (*Scaphiopus*) inhabiting southwest of USA in 10 days.

Urodeles are in a more advantageous position than anurans. During their long childhood they manage to grow almost to the size of their parents. However, the record of larva size belongs to the paradoxical frog (*Pseudis paradoxa*), found in the jungles of Guiana. Once they set up an alarm in the scientific world. It had been found that the tadpoles grew to a length of 25 cm, while that of the parents varied from 2 to 7 cm. The naturalists, who discovered it, assumed that it were the frogs who metamorphosed into tadpoles, and not vice versa. Everything was cleared up only in 1886, when Samuel Hormone managed to follow the full development of the tadpole. The paradoxical frog is not the only exception. The tadpoles of the midwife toad (*Alytes obstetricans*) and

toads of the genus *Pelobates* sometimes reach a length of 17-18 cm, while the adults are only 5 and 8 cm long respectively.

The young froglets leave the water and go to land but their development continues. In order to become parents it is necessary for them to grow up and to wait for the maturity of their sexual glands. The females of viviparous toads reach sexual maturity and mate at the age of 3 months, while the terrestrial frogs in the savanna of East Africa reach it 4-5 months after birth. Our northern amphibians do not proceed to reproduction during the second year of their life. The Siberian frog (*Rana cruenta*) becomes sexually mature only after 3-4 years at a minimum body length of 4.5 cm. The terrestrial frog (*Rana terrestris*) in the suburbs of Moscow starts reproduction at the age of 2-3 years, and the common frog (*Rana temporaria*) proceeds to it only after 3-4 years. The spotted (*Triturus vulgaris*) and crested (*Triturus cristatus*) newts in Sweden and Finland become parents only at the age of five years. The record of long development belongs to the olm (*Proteus anguinus*): it reaches sexual maturity only at the age of 14.

The development of urodeles is characterized by specific features, which distinguish them greatly from frogs and toads. Firstly, their development proceeds gradually, without any appreciable reconstruction of the organism, as in frogs. Secondly, they can manage without metamorphosis. It has been mentioned earlier that such a larva continues to grow and starts reproduction as if nothing has happened.

Limbless Miners

It is hard to imagine a miner without hands. However, many of those, who have chosen the eternal darkness of underground galleries as their habitat, completely lack

limbs. Recall, for example, the earthworm. This creature lacks even a skeleton though it is an excellent digger. It appears that limbs are a nuisance when digging not very wide corridors. It is not without reason that amphibians and reptiles abstained from limbs when adapting to life in the earth.

Legless amphibians belong to a special, very small order Apoda known as caecilians. Information appears from time to time in scientific literature on the discovery of new legless amphibians. Caecilians have been found during the last 10 years in Rio Muni (West Africa), Sao Tome and Principe Islands, etc. A new species of aquatic caecilians (*Inchthyophis*) has been found on the Java Island.

The order of caecilians presently includes about 50 species of extremely peculiar animals, whose appearance resembles big worms. The little head passes directly into a long wormlike body. The resemblance with a worm is stressed by the numerous annular grooves along the body. The annulate caecilian (*Siphonops annulatus*) has about 85-90 grooves at a body length of 40 cm, while the bigger legless Apoda (*Typhlonectes glutinosus*) may have up to 400. The bodies of aquatic caecilians (*Typhlonectes*) are slightly flattened on the sides. Caecilians are legless and tailless, and the resemblance to a worm is total. Even the cloaca is at the posterior tip of the body.

The length of caecilians is rather small, reaching only 30-45 cm and rarely more. The Thompson caecilian (*Caecilia thompsoni*), inhabiting the mountains of Colombia, is a giant: its body length reaches 120 cm. The miners are dressed quite modestly in an attire of dark and light brown, black or grey. This camouflage coloration helps in hiding. But there are some species with a light-blue and bright-yellow colouration.

Caecilians, more than any other amphibians, have preserved resemblance to the ancient, long extinct amphi-

bians and fishes: they have scales buried in the skin, the vestiges of scales that covered the bodies of their ancestors, amphibians with a carapace. It is not without reason that a whole group of these animals belongs to a family of scaled caecilians (*Caeciliia*). The heart of a caecilian is primitive: the only auricle is divided by an incomplete septum and has only one ventricle. The fish-type vertebrae carry the vestiges of a chord and short fins, which are quite numerous, i. e. 200-300, as in fish. But some features, in particular, the structure of the forebrain, indicate a higher development of the caecilians as compared to other amphibians.

Caecilians are confined to humid tropical regions. They occur in Africa, Asia, America, on the islands of the Indian and Pacific Oceans. Caecilians have not been discovered only in Australia and on Madagascar. They live in the earth, burrowing easily in the moist soil to a depth of 30-60 cm. Annulate caecilians inhabit anthills and termitaria, whose dwellers make up the basic item of their diet. Ichtyophis and aquatic caecilians are associated with water more than others. The former live in burrows along the banks of brooks and rivers, while the latter inhabit water bodies proper.

Caecilians are well adapted to underground life. They use their little strong heads like rams for burrowing into the soil. The long annulated body ensures good pushing through. This is promoted also by the abundance of slime, which is usually poisonous and is secreted by numerous glands of the skin, concentrated in the anterior part of each groove. The poison glands are distributed in aquatic caecilians along the entire body. This is evidently the reason why ants and termites are afraid of them and snakes turn away.

The mouth of the caecilian opens downward and does not become clogged with earth when the animal makes a tunnel. It has two small and very movable antennae on

the head, which the animal uses to investigate all the objects it meets, feeling the left- and right-hand parts of the space in front. It retracts the antennae into special pits between the eyes and nostrils when breaking underground roads. The holes of the big antenna gland are in the upper part of each pit. If the antenna is extended, then its base, which is pressed tightly to the pit, seals the holes. But when it is drawn in very deep, below the holes in the canals, the slime spills out freely and even sprays out at quick retraction of the antenna and compression of the gland. The purpose of the slime is to lubricate the movable organ. It is poisonous in many caecilians, who use it for defence and hunting. The poison in the secretion of the gland scares enemies away and can paralyze worms and small insects, preventing their escape in narrow burrows. If not for this device, the caecilians would suffer of hunger. It is not very easy for them to catch prey. The caecilian's tongue is immobile as it has fused with the jaw. The animal grasps its prey with its mouth and holds it fast with its jaws which have one or two rows of teeth turned backward. Special glands in the tongue secrete an abundant amount of slime to facilitate the swallowing of food.

Eyes are unnecessary in the underground habitat and for this reason they are underdeveloped, covered with skin or grown to the bone and, naturally, are ineffective. Hearing is quite mediocre. The external auditory pore is lacking and the internal ear is not connected with the exterior. Even the tympanic membrane is missing. Caecilians can hear only sufficiently loud sounds of a low frequency from 100 to 1500 Hz. But their olfaction is highly developed. Caecilians use it to find their food in the soil: insects, worms and small snakes. The larvae of aquatic caecilians (*Ichtyophis*), like other aquatic amphibians, have the organs of the lateral line on the head and body. In addition, these caecilians possess peculiar sensitive

ampullar organs in the anterior part of the head. Microscopic ampullae communicate with the exterior by a short canal, in which there are 15-20 sensitive cells. Zoologists assume that they are electroreceptors.

Caecilians breathe like any terrestrial creature. The only peculiarity is in the fact that they have a single right-hand lung. As in frogs, the air is pumped in by the movements of the oral cavity floor. The underground galleries, where the caecilians live, are poorly ventilated and one could easily suffocate there. It is not by chance that caecilians, who lead an underground mode of life, have a higher oxygen capacity of the blood and smaller erythrocytes than other amphibians. Hemoglobin saturates with oxygen more quickly in small erythrocytes and returns it to the body tissues just as rapidly.

Caecilians consume 4-6 times less oxygen at rest than during motion. The blood is unable to supply the required amount of oxygen and the animals use anaerobic respiration like other amphibians. As a result, aquatic caecilians can stay underwater for a long time though they receive through the skin a maximum of half the amount of oxygen normally supplied by the lung.

The breeding habits of caecilians are very interesting but they are poorly known. Unlike the most of apodidae, fertilization is internal. The cloaca of the male extends outside and turns into an intromittent organ, enabling true coition to take place. The cloaca of aquatic caecilians has special sucking cups that enable the mating pair to copulate in water. These suction cups are absolutely necessary for the animals because nothing else can make it possible for them to stay immobile next to one another, and it takes about three hours to perform successful copulation.

Many representatives of apodal amphibians bring forth their young alive. The female of the Central American caecilian (*Dermophis mexicanus*) in Guatemala car-

ries its 15-35 eggs for about a year. At the beginning of the rainy season, in May and June, she gives birth to tiny, very lively and viable young, 11-16 mm long. They grow very quickly and start reproduction at the age of 2 years.

Only 6-14 eggs develop in the oviduct of the female caecilian (*Typhlonectidae compressicanda*). When the reserve of yolk in the eggs is exhausted, the larvae emerge through the egg membranes, but remain in the mother's oviduct for a long time, feeding on the epithelium of its walls. The young have several rows of leaf-like teeth in their mouths. They use them to scrape the walls of their temporary shelter, thereby stimulating the secretion of a nutritive fluid, which is their main food. The mother also supplies them with oxygen. The larvae have gelatinous gills that they press to the walls of the oviduct in order to absorb oxygen. The walls of the oviduct are covered with branching villi in some viviparous caecilians. They grow very thick during pregnancy, greatly facilitating the supply of food and oxygen to the larvae.

The eggs of terrestrial caecilians develop on land. The 10-25 large, pea-sized eggs of the aquatic caecilians (*Ichtyophis*), inhabiting India, Shri Lanka and the Greater Sunda Islands, are covered with a tough membrane for protection against drying. Special outgrowths on the membrane ensure adhesion of the eggs, so that a cluster of eggs looks like a tight, compact mass. The female entwines the spawn with the rings of its body and broods it, wetting the eggs abundantly with its body slime. This fluid is partially absorbed by the eggs and their weight increases almost 4-fold during the brooding time. The eggs inevitably perish if they are left by the mother to the mercy of fate. External gills, rudiments of hind legs and a tail with a fin develop while the larvae are still in the eggs, as an indication of their affinity to amphibians, but all these appendages disappear by the time of birth. Water is entirely unnecessary for the majority of caecilians in their

development. Metamorphosis of the larvae occurs in the egg and then a tiny caecilian emerges, an exact copy of its own parents. Before its skin will dry, the young creature hastily burrows into the soil or crawls into a rotting stump, and begins its independent life.

The childhood of the aquatic caecilian's (*Ichtyophis*) larvae is longer. They need water for their final development and, therefore, search for a water body. They stay in the water for a definite period of time, during which they increase in length about 4 times and grow stronger. After they return to the land, they are true terrestrial creatures.

The Red Pages

Wildlife has been pressed greatly by the storm of technical progress and the demographic explosion. Certainly, it is not technical progress to blame. It is inevitable and necessary! The trouble is that mankind has realized too late the danger it is threatened with. The International Union for Conservation of Nature and Natural Resources (IUCN) has been created in 1948 to lead and coördinate the activities of state, scientific and social organizations in the majority of countries throughout the world. One of the first works, accomplished on the assignment of IUCN was a list of rare and disappearing species of animals and plants, as well as those threatened with disappearance, and publication of "Red Book" with the collected data. This publication has made it possible to compile a list of extraordinary measures needed to save the endangered species.

Simultaneously with the "Red Book", a "Black List" of animals and plants that have vanished since 1600 until the present time has been published. This date has been chosen not because animals and plants never became extinct before 1600. Recall the grievous fate of the Euro-

pean mountain goat that had been exterminated yet in the XII century. But scientific descriptions of animals and plants simply did not exist before 1600.

Amphibians are not mentioned in the "Black List". It is considered that not a single species of amphibians has disappeared during the last 1 or 2 millennia. This is explained by the great adaptability of the amphibians to ecological conditions, and also by the fact that they are of no interest to humans and have never been hunted with such persistence as, for example, the mountain goat. However, it is impossible to state with confidence that amphibians have experienced no losses. The absence of amphibians in the "Black List" is no indication that all is well. 35 species of amphibians are currently listed in the international "Red Book".

What are the reasons of the grievous situation of these species? There are several causes. The main one is the destruction of natural habitats, and 27 species of amphibians have suffered from this. Nature is supported, protected and certainly cultivated around big cities. Excessively thick undergrowth is cut down in suburban forests and, once dark and humid, they turn into light and dry forests that are attractive to the eye and accessible to everyone. These forests are a blessing for us, but they are too hot and dry for amphibians, and they lack reliable shelters. Amphibians disappear from these places, the further to the South, the quicker.

The main requirement for normal life of amphibians is the preservation of large and small water bodies where they breed. Numerous small and microscopic water bodies are destroyed when land is cultivated and highways are built and reconstructed, thereby reducing the number of places that can be used by amphibians for reproduction.

However, it is not enough to merely preserve the water bodies. It is vitally necessary for the amphibians that the

water therein should be suitable for the development of their eggs and the life of their larvae. It is not enough to prevent visible contamination of the water and stop the drainage of industrial and agricultural waste into the water. Frogs have disappeared almost everywhere in Western Sweden recently, the cause being an intensive rise of water acidity. Industrial enterprises discharge a great amount of sulphur dioxide into the atmosphere, where it is easily dissolved in rain to form sulphuric acid in combination with water. Acidity has increased most significantly in the water bodies of FRG and England. Terrestrial frogs (*Rana terrestris*) suffer more than others because their spawn is very sensitive.

Rivers, brooks and other water bodies, even in sparsely populated areas, come within the sphere of human activities more often than other natural objects, and these are usually harmful to amphibians. In Ladakh, a region high in the West Himalayas, the mountain rivers, constantly threatening with flooding and landslides have been turned into canals with concrete banks, and, as a result, several Alpine species of frogs have disappeared.

Amphibians have suffered great losses in Western Europe from highways. The areas covered by highways are not very great, but if the forest where amphibians live is on one side, and the water body where they spawn is on the other, then not many of them manage to cross a modern highway twice. A few years later the entire amphibian community is exterminated.

Adult amphibians are more resistant to poisons than birds and small mammals. But their spawn can either perish even at a minute concentration of any pesticide or develop into freaks. Cases have been observed of the mass death of sexually mature amphibians in poisoned water, or from eating insects and earthworms intoxicated by poisons. The poisoned frogs and toads become inert

and unable to hide; they are devoured by predators, who, in their turn, are poisoned too.

Human activities improve the living conditions of amphibians in extremely rare cases. The coco palm is cultivated on Jamaica and on other tropical islands. The heaps of coco shells, which accumulate near the plantations, have been used as safe shelters and breeding grounds for two native and two specially imported species of leaf-frogs. They all breed on the ground and need shelter from direct sun rays at this time. An expansion of the coco plantations has led to the thriving of the leaf-frogs.

Animals of many species are killed for their meat, fur, or beautiful feathers. Amphibians have not escaped this common fate. An enormous number of frogs are used for training students of medical and biological faculties, and for research work, and this caused a sharp decrease in their number in some European countries. England, France, Italy and FRG have been importing frogs for many years to meet this demand.

In countries, where frogs are an item of human diet, this has been the major cause for the decrease in their number. More than 200 000 of their own common frogs (*Rana temporaria*) are consumed annually in little Luxembourg. Edible (*Rana esculenta* and *Rana ridibunda*), Indian tiger (*Rana tigrina*) and many other species of frogs are also found in the diet of many peoples. The Goliath frog (*Rana goliath*) is hunted like common game with a bow and arrows in the old way. Hunting with a rifle is unreliable because a wounded frog can dive into the water, while a frog shot by an arrow is unable to move around.

Alpine toads (*Leptodactylus fallax*) have been preserved only on two islands of the Lesser Antilles. These big frogs make a dainty dish for the mountaineers, who do not have much meat. It is quite possible that Alpine toads will disappear into the stomachs of the native

population. The giant salamander (*Megalobatrachus maximus*) is threatened by the same fate. It has been an item of human diet in Japan and China from ancient times.

Collectors, lovers of domestic zoos, and those who cherish exotic souvenirs have become a true scourge of urodeles: lungless (*Desmognathus*), long-digit (*Ambystoma macrodactylum croceum*), blind (*Typhlomolge rathbuni*) salamanders in the USA, and a brightly coloured frog (*Atelopus varius zeteki*) in Panama. The olm (*Proteus anguinus*) has been caught only recently for the same purpose. Currently 10 species of amphibians suffer losses as a result of these activities.

Many frogs and salamanders suffer from their own relatives. Amphibians have adapted to each other in the existing biocoenoses, but the relations between native and imported species of amphibians, for example, between such big animals as a bull frog (*Rana catesbeiana*) and the marine toad (*Bufo marinus*) are quite tense. They clearly crowd in on the native small frogs, exterminating not only the insects but also a lot of tadpoles and young froglets.

The loss or deterioration of the food base is the cause of suffering for many animals. It has not occurred yet with amphibians. An adult frog can live in any small space in the centre of a modern city. But normal development of the young requires a certain minimum of food and the edible objects should be of suitable size. This is the reason why reproduction of amphibians is rarely successful in small gardens even if a pond is available.

35 species of amphibians are listed in the international "Red Book": 1.5 per cent of all those known today. Only 8 species are listed in the "USSR Red Book". Certain frogs and salamanders may be considered to be disappearing in our country though they are not listed in the

international "Red Book". The reason of this difference is quite evident: if the given species is on the verge of extinction in our country though it has been preserved somewhere else in adequate quantities, it is not easier for us.

Wildlife has suffered most in Western Europe. A total disappearance of amphibians is observed in industrially developed countries. 12 species of amphibians of the total number of 19 in FRG are on the verge of extinction. Hence, the legislation of some countries strives to preserve these animals. It is prohibited to kill and catch adult animals and tadpoles in France and Switzerland, exterminate their spawn, collect, sell, transport and relocate amphibians. The law concerns only native amphibians and permits to sell the animals if they have been bred in captivity.

It is easier to preserve amphibians than mammals and birds. They are unpretentious in most cases. Their habitat is very small. Large territories are unnecessary for their life and they are satisfied with a modest amount of food. They are not worried much by nervousness due to the presence of humans, which is so pernicious for most other animals. Finally, many amphibians have been made to breed in captivity.

It is not necessary to set up large reservations to save amphibians. Any little pond, tiny spawn or brook may be turned into a minireservation. Special financing is not required for their creation and it is quite simple for the local branches of the Society for Nature Conservation and for hobby groups of young zoologists or even for individual lovers of wildlife.

What do amphibians need to live well? First of all, it is necessary to take care of the water bodies. Even the smallest ones should be preserved so that newts, frogs and toads should have spawning grounds. If the water bodies are dirty, they should be cleaned out, and their conta-

mination by water from the fields, carrying dissolved fertilizers and pesticides should be prevented.

The amount of sulphur dioxide in the atmosphere should not reach a dangerous level. It is necessary to control acidity of the water. It is essential for newts that the pH, characterizing acidity, should range from 5 to 9. If the pH is less than 5, the pond should be treated with lime. The spotted (*Triturus vulgaris*) and crested (*Triturus cristatus*) newts which had not been seen since 1925 appeared again in 1970 in the regions of West Harz in the FRG. This is associated with the first success in purifying the atmosphere over industrial zones.

Many amphibians are killed on highways. When building new roads across the routes of amphibian migration, passages should be left under the roadbed and low screened fences be set up on the road sides. If it is impossible to do so, the road should be fenced in and catching cylinders buried in the soil. The trapped toads and frogs should be regularly collected and carried across the road. This measure is feasible for any school hobby group of young naturalists. It is still better to dig out a new water body for the suffering amphibians in order to eliminate their need to cross the road annually.

It is useful to dig out small ponds in arid regions. A pond is a splendid decoration of any garden or park, and many amphibians are so unpretentious that they can live next to humans. A population of the spotted newt (*Triturus vulgaris*) is flourishing in a small park of the Lenin-grad botanical garden, surrounded by urban construction. The ponds in the park are separated from the paths by wide lawns with thick grass, trees and bushes. The newts thus have a small and totally reserved territory, ensuring satisfactory living conditions. Amphibians disappear if the ponds in the parks are encircled with roads and the vegetation is exterminated at the water edge.

The XV General Assembly of IUCN, held in Christ-

church, New Zealand, in 1981 has been a major event in the conservation of animals. Work was completed there on elaborating the "World Strategy for Nature Conservation", which is intended for governments, governmental and international organizations as a guide for accomplishing different measures for nature conservation. It states, in particular, the necessity of including commitments to nature conservation in the national constitutions of each country. As is known, the USSR was the first state to include articles for nature conservation in the code of fundamental laws, the constitution. We have impressive experience in the field of nature conservation, for example, in recovering the number of elks, beavers, sables, reindeers, and others, who were practically on the verge of extinction, while today they are numerous enough to hunt.

We have earlier discussed many interesting amphibians: caecilians, salamanders, tree-frogs, toads, most common and most paradoxical frogs. It is worthwhile now to discuss some inhabitants of our country, whose fate is a matter of concern to Soviet zoologists. Their story should be known to everyone.

The Semirechensk salamander (*Ranodon sibiricus*) is the biggest one in the Soviet Union. Adult animals reach a length of 20 cm, though half their length is in the flat tail with a swimming fold on the back side. It has a flat wide head with a rounded snout. Its body is of dark-olive colour. The body of adult, sexually mature animals, is covered with dark blurred spots, and on the sides it has 11-13 grooves. The same grooves are found on the tail but they are less distinct. The forelimbs are tetradactyl and the hind ones pentadactyl.

The habitat of this salamander is in the Tien Shan chain, within the mountain range of Dzungarian Ala Tau in the Kazakh SSR and China at an altitude of

1800-2500 m in the zone of coniferous forests on the banks of brooks and little rivers, falling down from ledge to ledge. The salamander feels itself at home amongst the boulders and rocks in the creek bed washed out in the mountain, under stones and ledges overhanging a water stream.

The life of the salamanders is closely associated with water. They never travel far away from their native brook, but water is not their permanent habitat. When the gills degenerate in the larvae, they migrate to land, where they spend the light part of the day and return to water only to hunt. They find shelter in the burrows of voles, in cavities under stones and in rotting wood. The animals use the same shelter constantly, returning to it at dawn. The salamanders hunt quite successfully in water and on land. The choice of the hunting ground depends on the weather, the availability of food, and the individual habits of the hunter. When hunting in a water, the hunter thoroughly examines the parts of the brook with a calm current, swimming next to the bottom and studying the stones and crevices it encounters on the stony bed. Coming across a rapid or a waterfall, it goes ashore and bypasses the dangerous spot.

When the first autumn frosts begin, the animals stop surfacing and gradually migrate upstream, where the brooks dive under the stones and disappear underground, where the water does not freeze in winter. The animal stays there till spring. Amphibians, who were too late to reach winter quarters before the first frosts, get stuck at little waterfalls and rapids, and they spend the winter there often dying en masse of frost.

Reproduction of these salamanders has been discussed earlier. The female suspends big (up to 3.5 cm long) sausages of paired sacs with 25-50 eggs in each to the base of the paired spermatophore. The spermatozoa penetrate the double wall, reach the eggs and fertilize them. The

eggs swell gradually, becoming bigger from day to day, and three weeks later, when it is time for the larvae to hatch, increase in size to 18-20 mm, and the egg sacs reach a size of 20-30 cm. The larvae are small, only 15-20 mm long, but they have fore legs with two clawed middle digits. The hind legs appear much later, but their digits will also be armed with claws. The larvae need them to prevent the current from washing them away downstream to a big river. The young have webs between the digits that help them to swim and to attach to stones. The webs and claws degenerate in the adult animals.

The childhood of the larvae continues for 3 years and the period of youth extends for a further 2 years. The animals are sexually mature only at the age of 5 years. This is the Achilles' heel of this rare species. The young animals may come across many fatal accidents in the course of 5 long years, leaving no offspring behind.

The salamander evidently has no dangerous enemies with the exception of humans. Before the Great October Socialist Revolution the animals were caught and sent to China, where they were widely used in Chinese medicine. Even today the native population uses these salamanders as a medicine for curing malaria and for knitting bones in the case of fractures. It is difficult for this salamander to survive even when humans leave it alone. Spring floods and summer thunderstorms become natural calamity for it, when the brooks and rivers foam and flood the banks, washing away everything alive. Thus, the number of these salamanders is never very great. A normal density is 20-25 animals of different age per 100 m of brook. Direct sunrays are also highly dangerous because they kill the spawn, larvae and even adult animals.

Semirechensk salamanders (*Ranodon sibiricus*) are listed in the "USSR Red Book" and in the international "Red Book" of IUCN. These animals inhabit only one,

rather small territory, and they are few in number. It is prohibited to catch and kill these salamanders and it is planned to create a reservation in the basin of the Sarysu River.

These salamanders live very well in captivity. They like cool and tolerate warm water so long as direct sunrays do not fall on the aquarium. They are active in a shaded aquarium in the daytime. The animals are unpretentious in their diet and eat moths, earthworms and flour worms quite readily. Soviet zoologists must learn to breed these salamanders in captivity to guarantee preservation of the species. Beside that, they could become a laboratory test animal like the axolotl, making it possible to study the prospects of using them in medicine.

The Asia Minor newt (*Triturus vittatus*). Our amphibians are not very pretty. They may be graceful but their colouration is quite dull. But the Asia Minor newt in nuptial attire is beautiful. The size of the animals is 12-14 cm on the average. In spring their colouration is abundant in bronze-olive shades with dark and silver-blue spots and stripes, and their bellies are yellow-orange or orange-red. The high notched ridge, running from the back of the head along the body and turning into a caudal fin, gives the newt a most exotic appearance, resembling an American Indian with feathers in the hair. The females look more modest, but they are refined and graceful.

The newts live in the mountains at an altitude of 1000-2700 m. They inhabit Asia Minor, and within our country they are found in the Caucasus near the Black Sea coast (from the Krasnodar district to Adzharia). Surprisingly little is known of their life. Some scientists believe that they live in water all the year round, preferring pure flowing water, others think that they stay in water only in summer. Finally, a third group states that

the newts are interested in water only at the time of reproduction. Indeed, the newts appear in water for spawning at the end of March and in April.

The Asia Minor newt has no dangerous enemies but humans. The reduction of their number is due to the growing shortage of water bodies suitable for reproduction. The bright nuptial attire has played the newts a bad trick. It attracts the attention of females but it also makes tourists, who come to the water bodies in the spring, feel an itch to hunt them. Unwise children under school age and gray-haired experienced anglers, in fact everybody tries to catch the defenseless beauties and take them home. The captured newts are doomed and many of them perish before they reach the city. This is the reason why they have disappeared first near big cities and in localities visited by many people. To prevent a further decrease in the number of Asia Minor newts, it is necessary to stop any contamination of small brooks and rivers and to patrol the most accessible spawning grounds in spring in order to prevent the invasion of humans.

Asia Minor newts are found on the territory of the Borzhomi and Caucasian reservations. The newt is listed in the "USSR Red Book" as a rare species, inhabiting a limited territory.

The Ussuri clawed salamander (*Onychodactylus fischeri*) is a relative of the Semirechensk salamander (*Ranodon sibiricus*). It is a big animal. The size of adults varies from 15 to 21 cm. Its body is light-brown with blurred dark spots and it has 14-15 grooves like the Semirechensk salamander. Males are characterized by strong hind legs with a skin fold on the outside. The cylindrical tail is usually longer than the body. The larvae and some males, evidently those intending to start reproduction, have dark corneous claws on the toes. The characteristic feature of this salamander is the lack of lungs. When it

becomes adult and the gills degenerate, the animal uses dermal respiration in water and on land.

The clawed salamanders inhabit the Far East maritime territory and the Khabarovsk district in the Soviet Union, Korea and North-East China. They live in cool mountain brooks, which run through the thick shady forests, where the water temperature is a maximum of 10-12°C. They are intolerable to warm water and perish rapidly in it. The animals spend a greater part of their time on land and go into water only at dusk to feed. They migrate to the water in autumn when it turns cold at night, but before the beginning of winter they evidently go into the underground part of the springs, where the water never freezes.

The five volume edition of "Animal Life", which is very popular in this country, as well as handbooks and books on amphibians state that the females wake up in spring and lay paired egg sacs, containing 5-7 big eggs each. Apparently this is so. But nobody has ever managed to observe the behaviour of these animals during the breeding season. Scientists found females in summer with large yellow-orange eggs, that were visible through the light transparent skin on the belly. Autopsies have indicated that the females were not ready yet to spawn. An attempt to induce the reproduction process by stimulating the animals with hormonal preparations, as is easily done with fish and frogs, was a complete failure. Neither the salamanders kept in special cages in their native streams until the outset of winter, nor those taken by the scientists to Leningrad, showed any sign of reproductive activity.

Observing the life of salamanders in the Anikina lake, scientists have noticed that the adults disappeared somewhere in July. The larvae continued to live in the brook and seemed not to be worried by the absence of adults. Many small larvae appeared in the brook at the end of

July when the heavy showers came to an end in the mountains. Apparently the adults went to spawn in the underground part of the springs and the water currents washed the larvae out of the caves. The young had evidently just hatched out because their stomachs were still empty.

The smallest larvae were of 34 mm long. It is interesting to note the development of the lateral line organs. They extend even to the eye cornea, which confirms that the larvae spend the first days of their lives in total darkness. The female can bear a maximum of 18 eggs. Evidently only favourable living conditions during early, difficult childhood and the lack of dangerous enemies in the area of their habitat permits the clawed salamanders to survive with such a small number of offspring.

The scantiness of habitats and the low fertility of the Ussuri clawed salamander has been the reason for listing it in the "USSR Red Book". Its fate excites no apprehension because it lives in two reservations, namely, the Suputinsky and Kedrovaya lakes. However, it is necessary to ensure a comfortable life for the salamanders outside the reservations.

The Carpathian newt (*Triturus montandoni*) is not very conspicuous even during its nuptial period. It is quite small. The body of the animal is dark brown or brown with indistinct dark spots. The belly is orange. It has no ridge on the back and the tail fold, which is wider on the underside, adds no radiance to its general appearance. The indications of the male sex are the short, up to 1 mm thread-like outgrowth on the tip of the tail, which extends to 5-8 mm during the nuptial period, and the black soles on the hind legs.

The Carpathian newt is widespread in the Ukrainian Carpathians. It is found in forested mountains at an altitude of 150-2000 m. A few males may be found in spring

waiting for females in almost any pool. They reproduce also in lakes, though are more comfortable in small ponds.

The Carpathian newts set up their nuptial plays during the light time of the day and feed at dusk. When they finally leave the water, they stay at home all the day long and go out only in gloomy and rainy weather. The female lays the eggs on underwater plants, 2-4 eggs at a time, sometimes wrapping them up in leaves. The amount of spawn is very small, from 35 to 80 eggs, and rarely more. The larvae emerge 10-15 days later.

The newts feed on tiny insects, thereby doing some good. They spend the winter on land, burrowing under stones, into deep holes or rotten stumps. Carpathian newts have no personal enemies but they perish en masse in the case of early spring frosts. The newts are very sensitive to contamination of the water, including pesticides that are used for treating forests. The little animals are very sensitive to forest felling and disappear if all the trees are cut down.

The number of Carpathian newts began to diminish at the beginning of this century. It disappeared from the territory of the FRG before World War II. Its major habitat today is on the territory of our country, including the Carpathian reservation. Hence, it is listed in the "USSR Red Book". Efforts are being made to preserve its major spawning water bodies and to reduce the areas treated regularly with pesticides.

Caucasian salamander (*Mertensiella caucasica*). Very little information is available on this interesting animal. Its length is 18 cm and the cylindrical tail makes up 3/5 of its total length. The animal's body is brownish-black with yellow spots on the back, and the belly is brown.

Caucasian salamanders occur in the mountains at an altitude of 500-2800 m above sea level in Adzharia,

South-West Georgia and in the neighbouring regions of Turkey. They like to keep to the banks of brooks and little rivers. In the daytime they hide under stones, in clefts in the rocks and beneath fallen tree trunks or in shallow waters, from where the little animals stick out their heads. The salamanders are excellent swimmers, run fast over the ground and resemble brisk lizards. They drop their tails in case of need.

The salamanders hunt at dusk, catching insects, freshwater shrimps, wood-lice, earthworms, they also can find food in the water. They reproduce in the middle of summer in lagoons with weak currents. The females lay up to 90 big eggs, attaching them in clusters to the leaves of underwater plants. The population of these animals continues to decrease as a result of being hunted and water contamination. The Caucasian salamander is listed in the "USSR Red Book". It is studied and protected in the Borzhomi, Adzhametsky and Kintrishsky reservations.

The parsley frog (*Pelodytes caucasicus*) is elegant olive-coloured animal with dark-green spots and a white belly. In summer, when the frogs shed their skins and put on everyday clothes instead of festive attire, a light cross appears on the back as if someone has crossed the frog off the list of creatures inhabiting our Earth. The little frog carries its cross without a murmur.

Sexual dimorphism is clearly expressed in the frogs at the time of the breeding season. Corns grow out on the males, which are big, rough, velvety-black tubers on the shoulders, forearms, two digits of the fore legs and tiny tubers on the belly and chest. Numerous bent spines, necessary at the spawning time, appear on the tubers, across the body, on the back, and along the edge of the mandible. The females have an elegant waist and quite slippery skin. If it were not for the tubers and spines, the

male would be unable to hold his beloved tight at the most crucial moment and the spawn would not be fertilized. The frogs shed soon after spawning and the corns, like buttons on festive attire, remain on the shed skin, while the tubers remain on the respective spots of the body, but now they are smooth and slippery to the touch. Small, sparsely distributed red spots appear on the backs of some large species in the breeding season. And one more distinction: the males are slightly bigger than the females.

The parsley frog occurs in the Caucasian mountains at an altitude up to 2300 m and only in our country. They are extremely few in number. Their distribution is not even and they are found in several areas at great distances from one another: in the Krasnodar district, Georgia, Adzharia and South Osetiya. Only recently two new colonies have been found: on the slopes of the Rize range in Turkey near the border of the USSR and in North-West Azerbaijan.

The Caucasian parsley frogs live near water in shady, humid and cool forests. They prefer to spawn in stagnant waters, quiet back-waters or parts of rivers with a slow current. The development of the eggs requires warmth, therefore they spawn only in open areas which are well warmed by the sun. The frogs spend the light part of the day at the water edge, hiding under stones, in clefts in the bank or under overhanging thick grass. The males go into the water at twilight and start their call songs, inviting the females to follow them. The song comprises two parts and resembles a rattling lid on a tea-kettle.

The female attaches the spawn to fallen tree branches in the water. Each clutch comprises 8 clusters of eggs and resembles a cylinder strung on a wooden stick. The female spawns 300-500 eggs. Unlike our northern frogs, the breeding season of the parsley frogs begins in the middle of summer and ends in August. The tadpoles, that

emerged too late, lack the time required for metamorphosis and spend the winter in water. Hence, it is possible to find in the water both spawn and tadpoles that have developed through the first half of their childhood. They part with their tail at the end of summer and go to land.

The parsley frog has a lot of enemies, but the main ones are water snakes and humans. Economic activities near the water bodies deprive the frogs of their habitats and spawning grounds. If we consider the relatively small number of eggs laid by the frog and the unusually long and dangerous period of early childhood, it follows that the safety factor of the species is not great and any additional complications may cause extinction of the isolated populations in the individual habitats. The parsley frog has been listed both in the "Red Book" of IUCN and in the "USSR Red Book", because of the small number of their habitats and the appreciable decrease of their number in the last few decades. The frog lives in several Caucasian reservations. Measures for the recovery of the number of this species have not yet been planned, nor have comprehensive attempts been made to start breeding the parsley frog in captivity.

The Syrian toad (*Pelobates syriacus*) is an animal of average size. It is yellowish-gray on the back with dark-green spots on its smooth skin. Its belly is white-gray. The webs on the hind legs have big cuts. It occurs in Asia Minor, while in our country it is found in Georgia, South Armenia and South-East Azerbaijan. It lives in the zone of semideserts and Alpine steppes.

The Syrian toad is a close relative of the parsley frog but their modes of life are quite different. It spends the whole day burrowed into the soil at a depth of 10-15 cm. It burrows in surprisingly fast and disappears into the soil in 2-3 minutes.

The Syrian toad excels all its relatives in its ability to earth-working. The earth in its habitats is solid with rock debris and many big stones. The toads do a lot of digging. For some unknown reason they manage without a regular burrow. The animal starts digging every morning after hunting. It possesses two spades for digging, which are internal calcanean tubers on its hind legs, that make it easy to distinguish these toads from the parsley frogs that resemble them so much.

Living far away from water, they extract all the moisture they require from the soil, therefore they spend more than 20 hours a day burrowed in. Humid areas are very scarce in sunny Armenia at the height of summer, and much time is needed to suck the required amount of moisture out of the soil which is almost dry. They avoid wet areas in winter because it is warmer in dry soil as the heat conductivity of the latter is lower.

Mating occurs underwater. The spawn resembles two gelatinous sausages stuffed with ova, entwining underwater plants. The eggs develop in one week but the larvae start to feed only two weeks later and their early childhood is quite sedentary.

The toads travel to distant areas at the time of spawning because they avoid laying eggs in water that dries up in summer. The larvae develop fast and metamorphosis is completed in 2.5-3 months. By the end of the larval stage of development the tadpoles reach 13-17 cm, and the greater part of this length is in the tail.

The Syrian toad has suffered considerable losses during the last few decades. Owing to the cultivation of desert lands, the natural habitats of the toads have been destroyed and they have disappeared. They are secure against further encroachment of humans only in the Kyzylagach reservation. This has been the reason for their listing in the "USSR Red Book". Activities are under way currently to find suitable habitats for this animal

in order to settle it gradually in new areas. One of these areas is the shore of the newly-created Yerevan Sea. The Syrian toads have never occurred here before because the living conditions have been unsuitable. If their settling in this area is successful, the problem of these animals will be solved.

The running toad (*Bufo calamita*) is the smallest of the European toads. It is rarely more than 5-6 cm long in the North and 6-8 cm in the South. The animal has a greenish-brown skin with a dark-yellow stripe along the back, dark spots on the sides and a grayish apron on the belly. The attire is not much to look at and the toad is not very pretty. Its short hind legs are not in conformity with the toad's snout. Instead of leaping, the animal's locomotion is a peculiar trot, and it climbs very well. It can climb out of a deep hole, get onto a stump and walk up the rough bark of a slightly inclined tree trunk. It has no swimming webs but, nevertheless, it visits water and feels itself quite at home there, moving its legs in a peculiar manner while swimming.

The running toad is a nocturnal animal. It spends the day in basements, under stones or in the abandoned hole of some rodent, enlarging it if it is too little. When the soil is soft sand, the animal digs out holes, excavating the soil with the claws of its hind legs. The toad is unpretentious and devours anything it comes across, only its size should be appreciable. It is not squeamish about ants.

The running toad has numerous tiny and two large poison glands: on the head and the crura. If taken unawares by an enemy, it releases the accumulated secretion and becomes covered with a white foamy fluid with the sickly odour of burnt gunpowder. No enemy will wish to eat it.

The toads assemble in spring in water warmed up by the sun. The males inflate big resonating sacs on their

throats and start their nocturnal concerts. Their voices are loud, squeaky and one could hardly say that the music is charming. Spawning occurs at night. The female spawns two egg strings and tiny flat larvae hatch out on the third or fourth day. The tadpoles feed on silt, therefore the female lays the eggs even in holes filled with water where there is no vegetation. The tadpoles grow slowly and leave the water when they turn into small, lively toadlets. They spend the short, warm European winter burrowed in deep holes, in basements and greenhouses, and start to look for water at the beginning of spring. The toads reach sexual maturity at the age of 4-5 years and then produce their offspring. The running toad is common in amateur terrariums in England, Sweden, FRG. It is generally considered to be the cleverest European amphibian and it tries to justify this opinion. It is easily tamed and endures the misfortune of captivity without complaint.

Running toads occur all over Western Europe, except the most southern regions such as Spain, Italy and Greece, while in the East the borders of its habitat reach Minsk and the Carpathians. It lives also in South Sweden, in Ireland on the British Isles, on islands in the Baltic and North Seas. It is not fastidious and likes to settle on moorland, sandy dunes and swamps. Owing to its amazing adaptability, the running toad lived pretty well until recently, but today even those waste lands are within the range of human industrial activities. The toad is being deprived gradually of shelter and its number is decreasing everywhere.

Three species of the six amphibia common in England are capable of reproducing in waters on plateaux, namely, the spotted (*Triturus vulgaris*) and web-legged (*Triturus helveticus*) newts and the European common toad (*Bufo bufo*), are still relatively safe. But the species, who prefer low-land waters, for example, the crested newt

(*Triturus cristatus*), the common frog (*Rana temporaris*) and, most of all, the running toad (*Bufo calamita*) have lost the majority of their spawning grounds. They suffer from human industrial activities more than any other species.

The running toad is very rapidly driven away from waste lands, where sheep are no longer pastured and forests grown. The untouched heather grows thick, shaded areas appear, especially when the waste land is afforested. It is inconvenient for the running toad but becomes quite favourable for the European common toad and the latter drives out the previous owners of the territory.

Amphibians also disappear from littoral regions with the construction of beaches, roads and zones of recreation. Many small water bodies are destroyed for these purposes. The remaining swamps are drained and the ground water level drops, 70 per cent of the remaining water dries up in summer and the tadpoles perish. Biologists have calculated that the number of areas suitable for the life of amphibians on plains has been reduced by 99 per cent and in the valleys by 55 per cent. As a result, the running toad has disappeared from the South-West, South-East and central regions of England, and also from Wales and Northern Scotland. The same has occurred with the toad in Sweden and the FRG, Denmark, France and in other countries. It is doubtful whether further decrease of its numbers will stop.

The running toad is listed in the "USSR Red Book", though it is quite numerous in some regions of West Ukraine. The situation is complicated by the fact that the territory of the USSR is the extreme eastern area of its distribution.

The running toad lives in West Polesye in sandy dunes covered with grass vegetation, in pine forests, and in sandy quarries where the water never dries up. The animals do not avoid settlements. They live in orchards,

gardens, in melon fields. They like stone buildings and foundations and go into the basements of residential houses for the winter. The animals prefer sandy and clay-sandy soil. Reproduction occurs in small ponds and swamps with clear slightly alkaline water among sandy hills, containing neither iron, nor magnesium. The toads are not found on the territory of the Polesye reservation, and it is absolutely essential that they should adapt to our neighbourhood, where they are still living, should have water bodies suitable for reproduction and should have progeny every year.

The Hamilton frog (*Leiopelma hamiltoni*). The Leiopelmidæ include only a few species. The genus *Leiopelma*, related to the tailed frog (*Ascaphus truei*), mentioned earlier, occurs in North America, and the other species occur at the other end of the world, in New Zealand. These islands were discovered as far back as 1642 by Tasman, a Dutchman. The peculiar native fauna aroused much interest among Europeans and was studied comprehensively despite bloody wars with the native Maoris. The Europeans learned of the existence of these frogs there only 200 years after colonizing the islands.

Leiopelma hochstetteri was described first, but scientists have learned only recently that 3 species of closely related frogs occur in New Zealand. The second species was named *Leiopelma archegi* in 1942, and a third frog, discovered soon afterwards on one of the small islands of the archipelago, was named *Leiopelma hamiltoni*. The New Zealand frogs were named after the official discoverer of the species. All the three *Leiopelma* have been listed in the "Red Book" of IUCN since 1953. *Leiopelma hamiltoni* is the smallest species. It occurs currently only on two tiny islands, Mana and Stevens, in Cook Strait. The reason for the dramatic reduction of its number is unclear. The *Leiopelma* is most likely being exterminated

by rats brought to New Zealand by Europeans.

The embryonic stage is very dangerous for these frogs, because the eggs need 1.5-3 months for development, but then fully developed frogs hatch out with a tail as a symbol of childhood. The tail degenerates 2-3 months later when the frogs reach an adult stage.

Several thousand frogs of this species are currently inhabiting an area of about 15 hectares in the remaining forest on the Mana Isle. It is hardly possible to consider this last shelter suitable for their existence: a small forest open to oceanic winds with high temperature and humidity drops. The situation is still worse on Stevens Isle. Only about a hundred specimens survive in the woodless, elevated and rocky part of the island on an area of a few hundred square metres. The frogs are nocturnal animals and hide under stones in the daytime.

Rats have not yet invaded Mana and Stevens Isles. The New Zealand Agency for Nature Conservation must see to it that they do not appear on the islands. However, the poor strips of land, which are the last shelters of these frogs, are located near densely populated regions of the country, where there is an abundance of rats. No other amphibians occur in New Zealand, therefore the *Leiopelma* has attracted such profound attention as no other frog or salamander, in danger of extinction. Despite the apparent tragedy of the situation, the future of *Leiopelma hamiltoni* might be favourable because it can reproduce in captivity. A small and carefully watched laboratory population of the rare New Zealand genus of *Leiopelma* is in existence today. It has also been possible to breed *Leiopelma archegi*, but the very first New Zealand frog, *Leiopelma hochstetteri*, has not been so cooperative. Luckily, there is still a certain reserve of time. This "unmanageable" frog occurs in the mountains of North Island and its population is more numerous than that of the other two species.

Hardly anything is known of many amphibians listed in the international "Red Book". They are so few that it is impossible to observe their life under natural conditions. The fat toad (*Bufo arenarum*) relating to the family of white-lipped frogs is amongst the latter. It occurs in Australia and only four habitats of this animal are known in the West of the continent. They are all in the coastal zone amongst sandy dunes and splendid Australian beaches.

The fat toad is a nocturnal animal. It spends the day in a shallow, 10 cm deep burrow, which it digs out every morning anew in soft and humid sand. The earth-work is done very fast. Hardly anything is known of the toad's activities by night. One may conclude that it is not very active judging by the traces left on the sand. The maximum distance it covers daily is 28 metres, and the latter figure is the animal's record. The night journey is usually shorter. It has been impossible to learn the diet and breeding habits of the toad, or its mode of reproduction. The fat toad is assumed to be viviparous, because nobody has found its clutches of eggs and there is no fresh water in the areas of its occurrence.

The Colombian giant toad (*Bufo blombergi*) has been listed in the "Red Book". It occurs in Colombia and Ecuador on the Pacific Ocean slopes of the Andes. Despite its tremendous dimensions, reaching 21 cm in length at a weight in excess of 1100 grammes, it was discovered only in 1951 and it was immediately evident that it needed protection. Zoologists meet it very rarely in the wild. All that is known today of this giant toad, has been observed in the Los Angeles zoo, where they lead a satiated and calm mode of life.

The toad looks quite funny when hunting. The predator, flicking forward its tongue at a tiny helpless cricket, closes its eyes. This is an ordinary defence reaction, protecting the eyes in case the victim shows resistance. A

cricket is not dangerous, but for lack of time the animal is unable to discern which prey represents a menace.

The fate of the toad is not very grave today because it has been possible to breed it in Los Angeles. Evidently the time is near when the toad will be a common member of zoo communities and the extra young will be shipped to their native land in Colombia to recover the natural population.

The pine tree-frog (*Hyla andersoni*), that has almost disappeared from its native habitat in the areas of New Jersey and North Carolina, is suffering a calamity. It has been driven away by residential construction. The last tiny population of the black toad (*Bufo exsul*) is in the desert region of California. The long-digit salamander (*Ambystoma macrodactylum croceum*) evidently will not stay long alive at the coast of the same state.

The fate of the bright-coloured frog (*Atelopus virius zeteki*), which lives in the Anthony Valley in the mountains of Panama, is quite deplorable. The ancient inhabitants of the western hemisphere believed in a legend of the "golden frog", which lives in the eternally foggy mountains and bringing luck to the one who finds it. It is for this reason that golden articles, resembling frogs, were so widespread in pre-Columbian America, while badges with the image of the bright-coloured frog are manufactured now on an industrial basis. Unfortunately, the Anthony Valley is turning into a fashionable resort and each tourist tries to take a souvenir frog home. Rich Americans take back a live golden frog if they are lucky enough to find one, paying fabulous prices for them. Under these conditions it is very hard to arrange protection in order to save the frog of the American continent against greedy poachers. The golden frog has been exterminated almost completely today and it is practically impossible to meet it in the wild.

The red list of amphibians becoming extinct is not very long but there is nothing to be happy about. It is clear that other species will be added to the list as a result of thorough investigation of the living conditions of the salamanders and frogs. It is necessary, therefore, to render them effective assistance as soon as possible. Exhibitions of amphibians ought to appear at zoos, where they know how to work with wild animals, as has been done in Moscow and Leningrad. There are enthusiasts living in every city of our country who would help those working at zoos. The Society for Nature Conservation is one of the most popular social organizations in our country. Rare amphibians are beginning to appear in the large scientific centres of the country. The Leningrad zoo is apparently the only one in the world which has the Semirechensk salamanders (*Ranodon sibiricus*), which do not mate in captivity and this is extremely regrettable.

Amphibians need little for normal existence and we ought to do all possible so that the class of amphibians should not suffer any losses in species.

Always Vigilant

Amphibians render incalculable services to agriculture. Insects occupy the first place amongst pests that damage standing crops. The majority of frogs, tree-frogs, toads and salamanders feed on insects, some of them greedily devour mollusks, and finally, the largest amphibians are not to squeamish to eat rodents. Investigation of the amphibian diet in our country and worldwide has indicated that the insects they feed on are mainly destructive. Frogs and toads devour whatever they see more often and owing to the fact that insect pests are more numerous in areas of mass reproduction than any other insects, they

make up 80-85 per cent of all the food consumed by the amphibians.

Amphibians are the most versatile defenders of plants. Firstly, the range of readily eaten objects is very wide, excelling that of birds. Most amphibians have no firm food habits and swallow anything indiscriminately, the only condition being that the hunted prey should move and be edible, which is illustrated by the rich and varied diet of our northern frogs and toads. They happily eat locusts and weevils, bugs, click beetles, bark and various other beetles, including the Colorado potato beetle, and the caterpillars of different moths and butterflies. Fleas and leaf beetles make up a considerable part of the diet of tree-frogs. The latter also like mollusks. Secondly, unlike birds, amphibians are not very sensitive to poisons and therefore also feed on poisonous insects with an offensive odour and a bright, or to be more exact, frightening colouration. They do not abstain from certain caterpillars that are avoided by the majority of birds.

One more major feature of the hunting habits of frogs and toads has made them versatile predators. Insectivorous birds feed only in the daytime. Hence, their diet comprises only pests that are active at that time. Frogs and salamanders hunt round the clock: in the daytime, at twilight and by night. They render great service by exterminating nocturnal insects, which are not taken by birds.

Slugs are nocturnal enemies of plants. They are omnivorous creatures and feed on rye, wheat, clover, vetch, peas, pumpkin, carrots, cabbage, potatoes, tobacco, tangerines and lemons. It is evidently easier to list what the gluttonous mollusks do not eat because their appetite is excellent from early spring till late autumn. They penetrate into hothouses and greenhouses, invade strawberry fields and commit outrages there when the crop is maturing and it is impossible to apply any pesticides. Amphi-

bians do not shun slugs, while toads are their most active enemies.

Amphibians are versatile hunters. Some of them feed underwater or on the surface. Most of the frogs and salamanders hunt on land. Tree-frogs and tree salamanders, like birds, find their prey in the bushes and in the tree crowns. Their amazing hunting weapon, the tongue, enables frogs and tree-frogs to catch insects in flight. Our edible frogs catch their prey by leaping upwards, and tropical flying frogs do it on the "wing". Many amphibians have adapted to feed on the ground. Plants are protected by them from the crown to the roots.

Toads, frogs, tree-frogs and salamanders are very useful in exterminating blood-sucking insects: mosquitoes, flies, horseflies and gadflies, which are such a nuisance in summer. Among the blood-sucking insects there are many carriers of serious illnesses, for example, malaria. The flies, that inhabit our homes, carry dangerous microbes on their legs. Mosquitoes and flies are actively hunted by adult frogs and young froglets, and the tadpoles of newts, toads and aquatic frogs feed on the larvae and chrysalises of mosquitoes.

Of course, amphibians, like any other predators, are unable to exterminate completely the population of any pest, but they are not required to do this. It is sufficient that they sharply reduce the number of pests and maintain it at an average or even at a low level.

Amphibians are undoubtedly more efficient as destroyers of invertebrates than warm-blooded animals. Insectivorous birds are unable to survive long starvation, and their life is possible only at a body temperature of 39-41°C! It is quite a problem to maintain this temperature. Despite the warm attire of feathers, the small body of a bird cools down very rapidly. Birds spend a lot of biological fuel to keep their temperature, i. e. they must feed well. Even in the tropics, where it is summer all the

year round, birds spend a third of the available energy to maintain a constant body temperature. At any worsening of the weather, when it is frosty, rainy, or the wind is strong, the consumption of energy resources increases, though the replenishment of energy is sharply reduced. Insects hide and become inaccessible to birds when there is a drop of the ambient temperature. Hence, many birds perish of starvation in bad weather or are compelled to fly to other areas where the weather is better. Sudden spring frosts cause great damage to the population of birds. Adult birds may be able to survive brief periods of starvation but it is fatal for nestlings.

Birds determine the nutritive resources of the environment quite accurately. They settle in numbers which ensure reliable feeding for themselves and their offspring. They lay fewer eggs than usually if the year is expected to have unfavourable weather conditions and there will be a poor "crop" of insects. Fewer eggs are found in the nests of birds high up in the mountains, where nature is not very generous in food, than in the nests of the same species, dwelling in the valleys.

It is different with amphibians. They are unable to burn an increased amount of "fuel" and, consequently, raise their body temperature. Speaking figuratively, the fuel in their "ovens" is not burning, it is only smouldering. The animals must generate more heat than they lose so as not to cool down at a drop of the ambient temperature. Amphibians produce 30-40 times less excessive heat than warm-blooded animals. This economic consumption of energy enables amphibians to survive long dearth. Being satisfied with very little, they manage to survive hard times, staying half-starved for a month or two, not to mention brief periods of total starvation. In general, amphibians easily endure various adversities and their number remain stable.

The rate of biochemical reactions depends on the tem-

perature, therefore metabolism in amphibians fluctuates within a wide range, reducing when there is a temperature drop and intensifying when there is a rise of the ambient temperature. Thus, when it turns cold, the consumption of energy-active substances drops sharply instead of increasing. The colder the weather, the longer the amphibians can feed on their reserves. They manage without regular feeding even in the North, where they are active less than 6 months. Easily enduring a dearth or temporary cold weather, they take their opportunity when conditions turn favourable, feed well, grow intensively and accumulate strength for the next hard winter. This is a very significant distinction between birds and amphibians. Local birds increase their consumption of food very little at the time of most active reproduction of destructive insects. Amphibians, on the contrary, if the weather is favourable, sharply increase their feeding activities. In other words, amphibians are more reliable regulators of the number of pests than mammals and birds.

The life of amphibians is based on low energy consumption. Moderate energy requirements enable them to adapt to a constant insufficiency of food and utilize for life areas poor in food, which are quite unsuitable for birds and mammals. The low rate of metabolism and the ability to live permanently even in areas poor in food enable amphibians to play an essential part in the maintenance of biological equilibrium.

The lack of temperature control and, consequently, the insignificant consumption of energy enables amphibians to spend only 40 per cent of the energy resources of the consumed food for the vital requirements of their organism. The remaining 60 per cent is used for the build-up of their own body. Hence, amphibians are much more efficient producers of biological mass than warm-blooded animals, mammals and birds. Therefore, their role is so important in ecological systems. It is beneficial

to breed them for food. At equal expenditures for feed they ensure a considerably greater increment of products than warm-blooded animals.

The significance of amphibians in the protection of agricultural crops is well known. Investigations, carried out in industrially developed regions of West Europe, where very few amphibians have survived, have indicated that each 100 running toads in the FRG, by protecting potato, vegetable or rape fields against pests, ensure an economy of several thousand marks annually by saving means spent earlier on pesticides. Each animal can eat at least 100 000 pests.

Amphibians also fight quite effectively against pests on uncultivated land if their number is high enough. According to research data of recent years, the density of many amphibians in various geographical regions of our country is quite high, though it fluctuates. The number of edible frogs is 80-1165/ha, common frogs—50-1000/ha, European variable toads—25-300/ha, Siberian frogs—15-420/ha. The density of amphibians is not very great in the oak-groves of the Belgorod district. Only 60 terrestrial frogs, eating up to 100 grammes of insects daily, are found per one hectare of cultivated land. Their monthly ration reaches 3 kg, which is 5-6 per cent of all the insects, living freely on this territory. Individual species of insects, especially crepuscular ones, are exterminated by 20 per cent. And one must bear in mind that other amphibians also occur in these oak-groves.

The number of terrestrial frogs within the Volga-Kama basin is higher: 80-150/ha. They eat 190 000-336 000 different invertebrates annually, mainly vegetarian creatures in the broad-leaved forests and fir-woods. The density of amphibians is immeasurably greater in the tropics. Thus, representatives of only one species of wood frogs in Panama occur at a number of more than 1/m², which means about 11000/ha.

Europeans, who have cultivated these lands, brought many agricultural plants, unknown there earlier, and simultaneously introduced new destructive pests. Sometimes native insects have also started to exterminate the new crop and managed to breed at such a rate that the efforts of the farmers were reduced to naught. The most effective remedy in the fight against pests were amphibians, who sharply reduced the number of insect pests.

The marine toad has produced the greatest effect in regions with warm and temperate climates. This big and gluttonous amphibian feels quite at home on oceanic islands and saline soils, because it is better adapted to salt water than other frogs and toads.

Transplanting of marine toads started more than 40 years ago. It was brought from the Hawaiian Islands to North-East Australia in 1935, where it settled down in new areas and appeared in New South Wales in 1946, continuing to spread further South at an average speed of 2 km annually. The toads were brought to New Guinea in 1947 to fight against butterflies, who were pests of sweet potatoes. The toad occurs currently along the entire coast of the island, but it is not found at an altitude higher than 300 m above sea level. The area of the capital, Port Moresby, is the habitat of 3 toads per 1 hectare at the level of the humid forests, 30/ha occur in the savanna, and up to 300/ha live in settlements. The stomach of the toad is never empty. The average weight of the food in its stomach is more than 2 grammes. Evidently the toad is satiated only when it carries so much food inside. The main food of the marine toad at the cacao plantations in New Guinea and New Britain is snails and only partly ants.

The import of marine toads to the sugar-beet plantations on the Hawaiian, Bermuda, Phillipine, Jamaica, Barbados and Ryukyu Islands has been a success. Exter-

minating other pests, they contributed greatly to reducing the number of cockchafers.

Bull frogs spread through new territories very actively. Twenty-two pairs of these frogs were brought to Jamaica in 1967, and ten years later they had spread to all the swampy areas of the island. Settling sometimes meets with unexpected difficulties. Bull frogs, brought to Italy, reproduced and invaded quite big areas of the country, but their usefulness in protecting plants was minor because their number was very small everywhere. The reason of it is quite clear: the gastronomic habits of the Italians and the pesticides that are extremely harmful for the young frogs.

Amphibians cause harm only in extremely rare cases. Bull frogs have an adverse effect on pond farming. It is interesting to note that it is impossible to reduce the number of frogs in ponds, where the number of methods of fighting pests is restricted.

A bull frog is a big and gluttonous animal. Other species cause no harm to fisheries, and the fish farmers of our country need not worry about them. Only two species of edible frogs settle in large numbers in fish ponds in the USSR, mainly to the South of Moscow. They are very helpful because a major part of the edible frog's diet is made up of predatory water beetles and their larvae, which both feed on fish fry. Thus, the frogs are beneficial to our fish farms by exterminating the worst enemies of young fish. The frogs themselves are not very fond of young carp, which is the major object of our fish farming. The latter has been confirmed by a special investigation: only 44 fry were discovered in the stomachs of 275 frogs. Undoubtedly, the benefit, rendered by exterminating predators, exceed greatly the minor damage caused by frogs, occasionally eating the fry.

*Amphibians contribute actively to agricultural production and are bred in many countries on an industrial

level. Their cheapness and wide application make the frog and axolotl major laboratory animals, common objects of practical lessons at school, medical and biological higher educational institutions. Frogs constitute an item of human diet worldwide. The common frogs, which live in our ponds, are called "edible frogs" in Western Europe. It is both caught in the wild and bred in frog farms. The tiger frog (*Rana tigrinum*) of India and the aquatic green frog (*Rana hexadactyla*) are bred for the same purpose in Asia. They are known as an excellent delicacy. The blue-coloured frog (*Rana cyanophlyctis*) is not so delicious. It is widespread in mountain brooks and in ditches along roads, as well as in ponds on continental plains, where it is caught by nets and imported for laboratory use.

Amphibian breeding may be quite profitable. It should be borne in mind that, unlike warm-blooded animals, they use the greater part of the food for building up their body. It means that the increment of weight in the frogs is considerably greater per 1 kg of feed as compared with broiler chickens. The breeding technology is quite simple. Amphibians reproduce at any time of the year. It is only necessary to stimulate reproduction by ensuring optimum temperatures and placing them in spawning water bodies without using the expensive and laborious hormonal technique of stimulation. Artificial fertilization, which is usually practised at fish farms, is unnecessary.

It is better to incubate the spawn in special apparatuses, as in the case of fish, because it is easier to ensure the most advantageous oxygen and temperature conditions, prevent microbial and fungus infection of the eggs, control development and remove dead eggs in due time.

When breeding amphibians, it is hard to find food for adult frogs and the young, because the latter need small

live feed. Even in tropical countries, where insects breed very intensively, the amount of feed is usually insufficient for optimal growth. It is usually necessary to stimulate the reproduction and growth of the insects, or even to breed them artificially.

Industrial breeding of frogs has a long history, and it is continuously improved. A new method has been patented recently in Japan for growing edible frogs on small and large lung flies cultivated on domestic sewage.

An industrial method of breeding toads has been introduced in Vietnam. The animals are used for feeding snakes. Several serpentaria are functioning in this country, which are the only ones in the world where venomous snakes are bred on industrial level. The dwellers of the serpentaria need live feed and it has been necessary to set up toad farms nearby. Now they collect the poison of snakes and toads, which is exported mainly to Europe, while dried toads are shipped to the East: to Japan, Burma, Thailand. Dried toad meat is a valued remedy in traditional Eastern medicine.

Industrial breeding of amphibians has not yet started in our country. The Ministry of Agriculture of the Latvian SSR has been the first to display interest in setting up frog farms. Feed preparation is evidently the most difficult problem in organizing this new branch of agricultural production. It is doubtful that the dwellers of the farms will have enough natural feed under our changeable weather conditions.

One other difficulty, totally lacking in tropical countries, is the necessity to create favourable conditions for the winter season, which lasts in the Baltic republics for half a year. This season is most dangerous for the young offspring of the current year. The young froglets must grow up and gain strength to survive till next spring. Therefore, breeding should apparently be effected much earlier than in the wild, and the initial stages of growing

the tadpoles should be performed in enclosed and heated water. Nevertheless, let's hope that the breeding of frogs will be mastered and will not be less profitable than the production of poultry and pork.

Thus, amphibians are an object of agricultural breeding and participants in agricultural production. They are most vigilant protectors of meadows and gardens, fields, forests and even fish farms. They render tremendous, immeasurable benefit to the national economy.

It is not always very simple to consider the interests of the frog community, but it can often be done without considerable expenditures, if only some attention is paid to this animal, whose usefulness we are only beginning to appreciate.

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